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BIRD DISTRIBUTION ON THE SOUTH DOWNS, AND A COMPARISON WITH THAT OF SURREY GREENSAND HEATHS

BY L. S. V. VENABLES

(*With Plates* 8–9 *and* 1 *Figure in the Text*)

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1. INTRODUCTION

FROM east to west across the south-east counties of England runs a range of chalk hills known as the South Downs, which form one side of the jagged remains of a denuded chalk dome (Fig. 1). This southern side is wide enough to have been carved out into a bold array of steep-sided hills which run up to some 900 ft. above sea-level and stand well up from the intervening plain of Greensand heaths and the more fertile Wealden areas, between their abrupt northern scarp and the corresponding rise of the narrower North Downs. The hills are mostly flat-topped and frequently several miles in length.

It was on these downs that this investigation into bird distribution was conducted. From an ornithological viewpoint the plant associations were found to fall into eight main types (see below), and the bird distribution on each of these was studied. Woodland (mostly pine, oak and beech; pure or mixed) was not included, as such chalk hill woods have been dealt with in a general survey of British woodland birds (Lack & Venables, 1939).

The method used for obtaining the data given in Table 2 was that of

slowly walking a number of miles through each type and noting the birds seen. This not only showed which birds were occurring in which types but also, as the distance covered was recorded, afforded some basis for a rough quantitative comparison. The edge of any section, or places rapidly changing from one type to another in a short distance were avoided, it being an easy matter to find a large expanse of the same type (save in differentiating between open and closed scrub). A given grass phase would be found running along a hillside or hilltop for a considerable distance (Pl. 8, phot. 1), and the folds in these hills were not infrequently filled with patches of scrubland; though scrub was by no means confined to sheltered slopes.

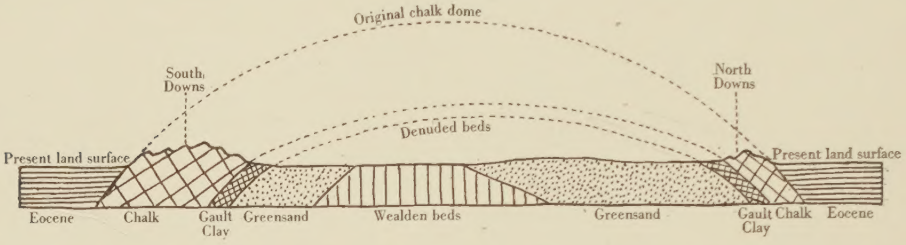

Fig. 1. Imaginary section through the Weald: the remains of the denuded chalk dome stand up in abrupt scarps. Vertical scale much exaggerated.

As this study is concerned with the breeding season only, the birds are dealt with—both in the tables and in the text—as pairs, never as single birds. In practically every case, however (except with game birds), this was checked in other ways, as by both birds being seen or heard, male in song, nest found, bird betraying much anxiety and thus presumably having a nest, and so on. For the sake of simplicity in the tables, single pheasants and cuckoos are also referred to as "pairs", although, in fact, the former is usually polygamous, and the latter usually polyandrous. Obvious non-breeders such as gulls, rooks, swifts, etc., were not counted.

The data given in Table 2 were obtained during the last few days of April and the first week in May 1938, and only at times of day and conditions of weather when the birds could be expected to be reasonably active and conspicuous. The walks were made between the Midhurst-Chichester road to the east and the Meon Valley to the west. Many points were checked and some of the juniper scrub was covered, however, later in May in the vicinity of Leckford, Hampshire (by kind permission of Mr J. Spedan Lewis); and, in previous years, visits had been paid to the Berkshire Downs and the Chiltern Hills.

Owing to the fact that the data in Table 2 were obtained in the early part of the spring, possibly such late migrants as turtle dove and nightjar were missed. I have found the nightjar breeding in open thorn-elder scrub on the Berkshire Downs, and Ingram & Salmon (1924) record the turtle dove as

being, under certain conditions, essentially a scrub-nester. However, the nightjar is very inconspicuous owing to its nocturnal habits, and the turtle dove at Leckford was confined almost entirely to the tallest hedgerows.

2. THE BOTANICAL PHASES

(a) Chalk

These fall into eight main types which are as follows:

Grass. The grass on the hills is practically untouched by man: it is mostly grazed but not cut. The "cultivated" grass (fertilized, chain-harrowed and mown) in the valleys between the hills was avoided, because as natural a grass formation as possible was desired for the purpose of comparison with the natural heather heaths of Surrey Greensand. This hill grass was divided into three types:

(1) *Thick grass with occasional bushes* (Pl. 8, phot. 1). Grass mostly ankle deep with tufts up to knee height in places. Occasional scattered bushes of thorn, elder, yew or juniper. This is not unlike the well-known Savannah formation which is so extensive in many parts of the world.

(2) *Sparse grass with occasional bushes* (Pl. 8, phot. 2). Short-cropped turf, frequently with patches of bare earth and rabbit holes—the rabbits being one cause of the shortness of the turf. Tufts even ankle deep were rare. Occasional bushes as in (1).

(3) *Sparse grass.* As in (2), but without the bushes.

Scrub. As distinct from evenly planted man-made plantations, the scrub areas of the South Downs showed a good deal of variation—it was not common for a stand to be constant over any considerable area. An attempt was made to keep "Open" and "Closed" distinct, but this distinction must be somewhat arbitrary at times; closed stands had some parts open, and vice versa. Also, no stands in these "natural" areas were quite pure. The deciduous areas had a few definitely dominant species (these are given) and the evergreen areas had as well-marked dominants either yew or juniper. These were kept separate but it should be understood that a few deciduous bushes (frequently elder) were always present.

The height, too, was very variable—from young, low bushes up to 25 ft. or more in the case of the yew, and mostly 6–12 ft. with the juniper (Pl. 9, phot. 5). The thorn scrub ranged up to 15 ft., a few shrubs being taller and many shorter.

The ground vegetation of the scrub areas frequently varied too much in a small distance (i.e. in a single nesting territory) to make it possible to define it. As a general rule, however, evergreen scrub had sparse ground vegetation—often none in closed scrub; and deciduous frequently had good vegetation, though this varied in different places from short rabbit-cropped turf to rich patches of brambles and bracken.

(4) *Closed thorn scrub.* Thorn dominant (*Crataegus oxyacantha* and *Prunus spinosa*) with some elder, bramble and gorse in places. The bushes ranging up to 15 ft., a few taller and many shorter. Patchy ground vegetation (see above).

(5) *Open thorn scrub* (Pl. 8, phot. 3). As in (4), but in open formation.

(6) *Closed yew scrub* (Pl. 9, phot. 4). Dense yew with occasional admixture of other species. From young, low bushes up to 25 ft. or more. Mostly bare earth beneath but short grass in places.

(7) *Open yew scrub* (Pl. 9, phot. 4). Similar to (6) but in open formation. Frequently with a carpet of short grass.

(8) *Open juniper scrub* (Pl. 9, phot. 5). Very open formation of dominant juniper bushes; 6–12 ft. high with occasional seedlings. Sparse grass ground vegetation as in (2) and (3).

In the thick hedges of the cultivated valleys the lower part of the "scrub" was, on the average, much thicker than in the natural scrub stands of the hills. This difference was reflected in the avifauna of the dense, artificial hedge-scrub of the lowlands. The low-nesting yellow and cirl buntings were both more numerous than in the hills, and corn buntings (*Emberiza calandra*), too, were not uncommon though entirely absent from the downland counts. On the Berkshire Downs and at Leckford, however, I found them in typical type 1. (On the Berkshire Downs near Lambourne I have crossed a wide expanse of rich grass without any bushes. Jumps for training race-horses have been erected, however, and the corn bunting has come in as a breeding species, the males using the jumps as song-posts.) Some lesser whitethroats (*Sylvia curruca*) were seen at the valley hedgerows but none was encountered in the hill scrub though this species, too, was breeding in open thorn scrub (as type 5) on the Chilterns. The tall valley trees accounted for the presence there of tree pipits (see Venables, 1937).

(a) Greensand

For the purpose of comparing chalk and Greensand bird distribution some figures from typical Greensand scrub are appended. The greater density near the ground, especially in the gorse scrub, is reflected in the greater numbers of such birds as whitethroats that nest just above ground level.

(9) *Pine scrub.* Closed to open; very variable. 6–12 ft. pines with occasional gorse bushes and tall pine or birch trees. Heather ground vegetation; mostly thick and frequently knee high.

(10) *Gorse scrub.* Dense patches of gorse bushes up to 6 ft. high. Mostly thick, tall heather between, but bracken and grass in places. Occasional birch or pine trees.

(*Natural birch scrub.* The scattered patches of thin birch saplings afford little or no actual cover and apparently merely bring in the song post species (see Venables, 1937). Chaffinches and even, on rare occasions, nightingales breed in the thicker patches, but these were too small to afford a reasonable count.)

3. Discussion on bird distribution

(a) Chalk

It is not proposed to enter into a lengthy discussion here, as all the data are given in Table 2. Some of the more striking points are these:

General. Taken as a whole unit, the three grass phases showed a marked difference from the scrub phases. Not only had the former largely different species but a smaller variety and less birds per mile. This is to be expected,

Phot. L. S. V. Venables

Phot. 1. Type 1: Hill of thick grass with occasional bushes. Shows large expanse of single vegetation type.

Phot. L. S. V. Venables

Phot. 2. Type 2: Sparse grass with occasional bushes. Note the frequent patches of bare earth.

Phot. L. S. V. Venables

Phot. 3. Type 5: Open thorn scrub.

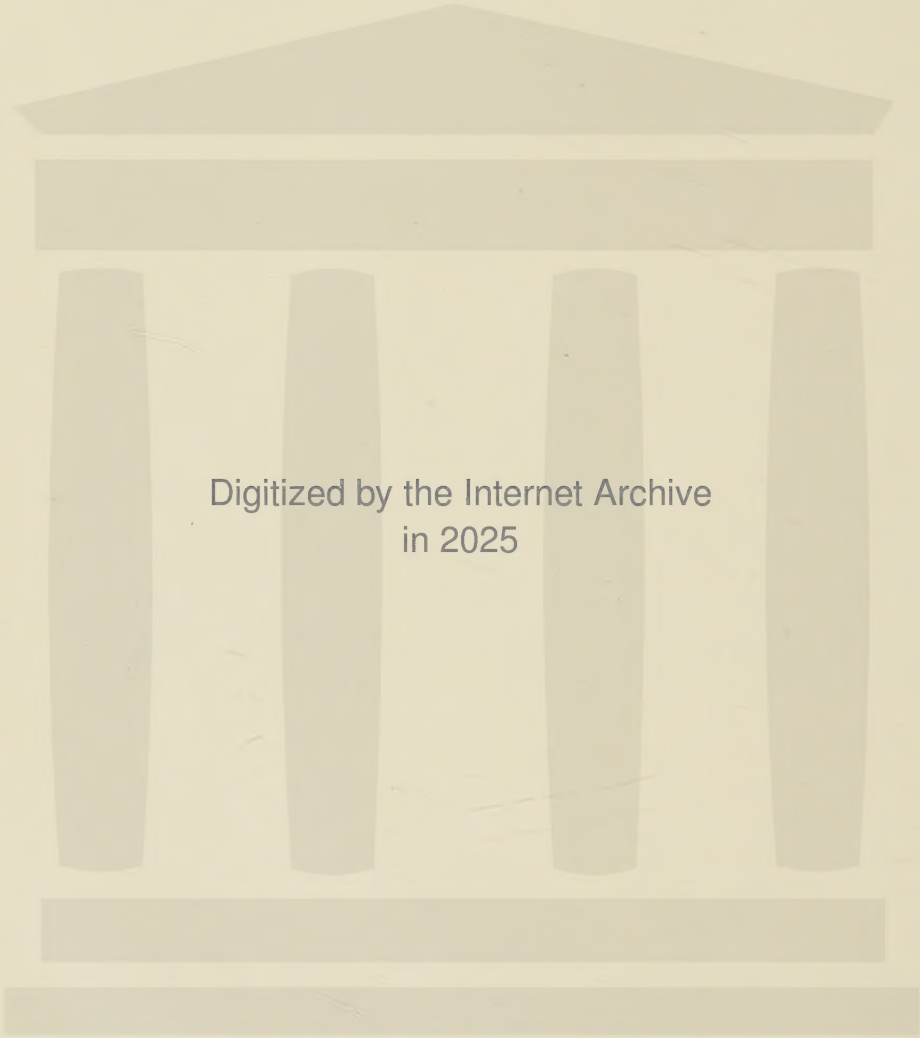

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Table 1

	Chalk								Greensand	
Vegetation type ...	1	2	3	4	5	6	7	8	9	10
Description ...	Thick grass with bushes	Sparse grass with bushes	Sparse grass	Closed thorn scrub	Open thorn scrub	Closed yew scrub	Open yew scrub	Open juniper scrub	Pine scrub	Gorse scrub
Miles counted	6	7	6	3	4	4	3	3	3	3
Pairs per mile	20	13	12	43	42	24	27	14	12	22
Total number of species	8	15	6	20	21	16	20	12	12	14

as the grass phases had only one "layer" of habitat, so to speak, and the scrub phases more. The open juniper scrub is an exception, but this was so very open (Pl. 9, phot. 5) that it really was not very different from type 2 (sparse grass with occasional bushes, Pl. 8, phot. 2). A few scrub species came in with the scattered bushes of types 1 and 2, but not nearly so many as might have been expected. The converse was also true: much open scrubland had ground vegetation very similar to types 1, 2 and 3, but the typical birds of the latter phases (skylark, woodlark, meadow pipit, wheatear, stone-curlew and lapwing) were not found there (except in open juniper scrub). If nest site, nest material and food were the only limiting factors there appears to be no ecological reason, save possibly that of food, why a bush-nester could not nest in a single bush on a large expanse of grass, and no reason at all why a ground-nesting "moorland" bird could not nest in a small grass patch in scrub. The psychological aspect of bird distribution has been discussed by Lack (1933), Lack (1937), Lack & Venables (1937) and Venables (1937). It would seem that not only must each individual species have its special nest site, but the actual appearance of the territory as a whole must "look right". Table 2 shows that it was rare for a bush-nester or -singer to be found breeding where there was not a great number of bushes (i.e. scrub), and for a ground-nester and air-singer to nest where there was not a big expanse of grass and much open air space immediately above it.

Grass. The thick grass had a higher density of birds than the sparse grass phases, but the latter, together, had a greater variety of species. The habitat selection of some birds was very marked. The meadow pipit was numerous in the thick grass (seven pairs to the mile), but only one pair was seen in 13 miles of sparse grass. The skylark nested freely in sparse grass but was twice as numerous in thick grass. Conversely, there were seven pairs of lapwings to the mile in sparse grass but only one pair was found in 6 miles of thick grass; the six pairs of stone-curlew and the 20 pairs of wheatears were all in the sparse grass and none in the thick; and the four pairs of woodlarks all in sparse grass with song posts. These figures include the open juniper scrub where an overlap community was found. The scattered bushes of types 1 and 2 introduced only a very few bush birds: all were less than one to the mile.

Table 2

Vegetation type	Chalk (grass)						Chalk (scrub)										Greensand (scrub)			
	1 Thick grass with bushes		2 Sparse grass with bushes		3 Sparse grass		4 Closed thorn scrub		5 Open thorn scrub		6 Closed yew scrub		7 Open yew scrub		8 Open juniper scrub		9 Pine scrub		10 Gorse scrub	
Miles counted	6		7		6		3		4		4		3		3		3		3	
	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs	Pairs per mile	Total pairs
Carrion crow (*Corvus corone*)	.	.	.	.	.	.	1	2	×	1	×	2	×	1	.	.	.	.	.	.
Magpie (*Pica pica*)	.	.	.	.	.	.	1	3	×	2	1	4	1	3	.	.	.	.	.	.
Greenfinch (*Chloris chloris*)	.	.	.	.	.	.	×	1	1	3	.	.	×	1	2	6	.	.	.	.
Chaffinch (*Fringilla coelebs*)	.	.	×	2	.	.	8	23	8	33	6	25	8	28	3	10	2	5	×	1
Linnet (*Acanthis cannabina*)	×	2	×	1	.	.	2	5	2	6	1	3	3	8	2	6	.	.	2	6
Yellow bunting (*Emberiza citrinella*)	1	4	.	.	.	.	×	1	1	4	.	.	×	1	1	2	×	1	1	2
Cirl bunting (*Emberiza cirlus*)	.	.	.	.	.	.	×	1	.	.	.	.	.	.	.	.	.	.	.	.
Skylark (*Alauda arvensis*)	10	59	3	23	5	29	.	.	.	.	.	.	.	.	1	3	.	.	×	1
Woodlark (*Lullula arborea*)	.	.	×	3	.	.	.	.	.	.	.	.	.	.	×	1	.	.	.	.
Tree pipit (*Anthus trivialis*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	1	2
Meadow pipit (*Anthus pratensis*)	7	40	×	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Goldcrest (*Regulus regulus*)	.	.	.	.	.	.	.	.	.	.	2	8	2	6	.	.	×	1	.	.
Great tit (*Parus major*)	.	.	.	.	.	.	×	1	×	2	×	2	1	3	.	.	.	.	.	.
Coal tit (*Parus ater*)	.	.	.	.	.	.	.	.	.	.	1	5	.	.	.	.	×	1	.	.
Marsh tit (*Parus palustris*)	.	.	.	.	.	.	.	.	×	1	.	.	.	.	.	.	.	.	.	.
Willow tit (*Parus atricapillus*)	.	.	.	.	.	.	.	.	×	1	.	.	.	.	.	.	.	.	.	.
Blue tit (*Parus caeruleus*)	.	.	.	.	.	.	.	.	.	.	.	.	×	1	.	.	.	.	.	.
Whitethroat (*Sylvia communis*)	.	.	.	.	.	.	1	3	2	8	.	.	.	.	.	.	1	2	8	25
Blackcap (*Sylvia atricapilla*)	.	.	.	.	.	.	×	1	.	.	.	.	.	.	.	.	.	.	.	.
Dartford warbler (*Melizophilus undatus*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	4	1	3
Willow warbler (*Phylloscopus trochilus*)	.	.	×	1	.	.	8	25	9	35	1	4	1	2	.	.	4	13	3	8
Chiffchaff (*Phylloscopus collybita*)	.	.	.	.	.	.	.	.	.	.	×	1	×	1	.	.	.	.	.	.
Mistle thrush (*Turdus viscivorus*)	.	.	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.
Song thrush (*Turdus ericetorum*)	.	.	.	.	.	.	1	4	2	6	.	.	×	1	.	.	.	.	.	.
Blackbird (*Turdus merula*)	.	.	×	2	.	.	8	23	7	27	3	12	4	11	2	6	.	.	1	2
Robin (*Erithacus rubecula*)	.	.	.	.	.	.	5	16	4	16	4	15	3	9	.	.	1	3	1	2
Nightingale (*Luscinia megarhyncha*)	.	.	.	.	.	.	.	.	×	2	.	.	.	.	.	.	.	.	.	.
Stonechat (*Saxicola torquata*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	1
Wheatear (*Oenanthe oenanthe*)	.	.	2	11	1	7	.	.	.	.	.	.	.	.	1	2	.	.	.	.
Dunnock (*Prunella modularis*)	.	.	.	.	.	.	2	6	2	8	1	4	1	2	.	.	1	2	2	6
Wren (*Troglodytes troglodytes*)	.	.	.	.	.	.	1	2	×	1	×	1	×	1	.	.	.	.	1	3
Green woodpecker (*Picus viridis*)	.	.	.	.	.	.	.	.	×	1	×	1	.	.	.	.	.	.	.	.
Cuckoo (*Cuculus canorus*)	1	5	1	6	×	2	.	.	1	4	.	.	×	1	1	2	×	1	1	3
Little owl (*Athene noctua*)	.	.	×	1	×	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Kestrel (*Falco tinnunculus*)	.	.	.	.	.	.	×	1	.	.	.	.	.	.	.	.	.	.	.	.
Stone curlew (*Oedicnemus oedicnemus*)	.	.	×	3	×	2	.	.	.	.	.	.	.	.	×	1	.	.	.	.
Lapwing (*Vanellus vanellus*)	×	1	4	29	5	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stock dove (*Columba oenas*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	1	.	.	.	.
Ring dove (*Columba palumbus*)	.	.	.	.	.	.	2	7	1	4	2	9	1	3	.	.	.	.	.	.
Pheasant (*Phasianus colchicus*)	×	3	×	1	.	.	1	2	1	3	×	1	×	1	.	.	×	1	.	.
Red-legged partridge (*Alectoris rufa*)	.	.	×	2	.	.	.	.	.	.	.	.	×	1	.	.	.	.	.	.
Common partridge (*Perdix perdix*)	1	5	×	3	.	.	.	.	.	.	.	.	.	.	×	1	.	.	.	.

× = less than one pair per mile (0·6 = 1).

Scrub. As in evergreen *versus* deciduous woodland, the evergreen scrub had a lower density of population than the deciduous. The variety of species, however, was about the same but slightly less for closed yew. This, perhaps, is not surprising, the dense foliage (Pl. 9, phot. 4) causing a dark, gloomy interior with little cover save in the thickly interlocking canopy, while of ground vegetation there was little or none. An interesting point is that in this, the tallest formation, the chiffchaff came in as a breeding species, whereas the closely allied willow warbler was well distributed throughout all the scrub. As is pointed out by Lack & Venables (1939) the former species demands a higher song post than the latter.

The goldcrest and, to a lesser extent, the coal tit were quite common in yew but absent from thorn. Lack & Venables (1939), show that this is also true of woodland; the goldcrest especially predominating in conifer, i.e. evergreen woods. On the other hand the willow warbler and, to a smaller extent, the blackbird were a good deal more numerous in the deciduous scrub. The ubiquitous chaffinch ranged in more or less equal numbers through them all.

Only small patches of closed juniper scrub were found during the census taking; these were too small and uncommon to give a reasonable amount of data. Lack & Venables (1939), however, give some figures for a stand of 4–10 ft. juniper bushes, dense in places, near Salisbury. The birds found there, in numerical order of observed frequency, were chaffinch, blackbird, willow warbler, goldcrest, yellow bunting, cirl bunting, linnet, song thrush, dunnock (hedge sparrow) and little owl. This list agrees well with the species seen in the small patches during the present investigation and it would seem that closed juniper scrub is, as regards its avifauna, much the same as closed yew scrub, if one takes into consideration the comparatively lower and smaller bushes of the former.

The scrub community had a considerable overlap with what are usually considered woodland species, showing that the large trunks and branches are not really necessary for such birds: the make-up and, presumably, general appearance of a scrub stand of bushes sufficing. The canopy-nesting carrion crow, magpie and kestrel; the lower-nesting ringdove; and the hole-nesting green woodpecker and tits, all featured in the counts; but Lack & Venables (1939), in discussing British woodland, say that in this country at the present day, with the almost complete lack of natural stands of trees and bushes, it is very difficult to differentiate between woodland and scrubland species. The data given in Table 2 show that the latter community embraces many species usually met with nowadays in the vicinity of large trees only. As, of course, there were less holes suitable for tits in the scrub bushes than in big trees, so too there were correspondingly less tits. It is perhaps not surprising that the green woodpecker was the only woodpecker encountered in this scrub. It seems to be forsaking woods and becoming a ground-feeder. It is only logical, therefore, that it should forsake large trees for nesting.

Lack and myself have already discussed the psychological points of habitat selection and their influence on bird distribution. These points include such features as the high post demanded by some species for the male to sing from—although perhaps not demanded by a closely allied species; the apparent inability of an individual species to breed save in a certain type of nest in a certain type of place, while there is usually no apparent physical reason; the preference for sparse ground vegetation of some ground-nesters, and for thick of others, and so on.

(b) Comparison with Greensand heaths

In a previous contribution to the subject of bird distribution (Venables, 1937) it was pointed out that the birds there described should be studied in another environment and the distributional limiting factors in the two places compared. It was in part for this reason that distribution on chalk hills was investigated in 1938. Environmentally, both situations have much in common —dry soil with a ground vegetation rich, moderate, or almost absent; and single bushes or patches of scrub. Both are more or less natural communities and very little interfered with directly by man.

Comparison of botanical phases. These have already been described for the Surrey Greensand heaths (Venables, 1937) but are briefly summarized against the similar chalk hill phases as follows:

Greensand, phase 1. Bare earth after fire. A parallel to this was not seen on the chalk.

Greensand, phase 2. Patchy vegetation, frequently short, and patches of bare earth. This is much the same as types 2 and 3 of the chalk—sparse grass with patches of bare earth, and with or without scattered bushes. The bushes on chalk type 2 are alive and would do for a bush-nester, but those on Greensand phase 2 are fire-killed and would do as song posts only.

Greensand, phases 3 and 4. 3 is moderate heather growth and 4 is rich (18 in. to 2 ft.) heather with bushes and saplings standing well up. These two may be taken roughly to equal chalk type 1; rich grass, ankle deep with knee-high tufts, and scattered bushes.

The scrub stands, on the other hand, are a good deal different in that both the Greensand types (gorse and pine) have a rich ground vegetation of full-grown heather and the gorse is dense from ground level right up to the top. On the chalk, the thorn scrub has good ground vegetation in places and sparse in others, while the latter is generally poor in open juniper and open yew, and very frequently completely absent in closed yew.

Avifaunal comparison. The following species occurring both on chalk downs and Greensand heaths have, as far as possible, similar habitats:

Carrion crow. Nest built in a tree on Greensand and in the tallest scrub (thorn and yew) on chalk.

Chaffinch. Bush or tree for nesting and song post. Occurred in small numbers with scattered bushes but very numerous in scrubland on both chalk and Greensand.

Linnet. As the last, save that much of the singing takes place in company or while flying about and appears to have almost no territorial significance (see Tucker, 1938).

Yellow bunting. Thick lower vegetation for nesting, and a song post—chalk and Greensand.

Phot. L. S. V. Venables

Phot. 4. Types 6 and 7: Closed yew scrub in foreground; open yew scrub behind.

Phot. L. S. V. Venables

Phot. 5. Type 8: Open juniper scrub.

Face page 234

Table 3

	Greensand		Chalk
	Phase	Scrub type	type
Carrion crow	1–4	.	4–7
Chaffinch	4	9–10	2 4–8
Linnet	4	10	1–2 4–8
Yellow bunting	4	9–10	1 4–5 7–8
Skylark	2–4	10	1–3 8
Woodlark	1–3	.	2 8
Meadow pipit	4	.	1–2
Goldcrest	.	9	6–7
Coal tit	.	9	6
Whitethroat	4	9–10	4–5
Willow warbler	3–4	9–10	2 4–7
Blackbird	.	10	2 4–8
Wheatear	1–3	.	2–3 8
Dunnock	.	9–10	4–7
Wren	.	10	4–7
Cuckoo	3–4	9–10	1–3 5 7–8
Kestrel	2–4	.	4
Stock dove	1–4	.	8
Pheasant, Red-legged partridge, Common partridge	See context		

Skylark. The fondness for grass (see Lack & Venables, 1937) is well shown in the chalk figures, as is also the fact that this species was quite numerous on even sparse vegetation with patches of bare earth, as in the heathland habitats. It was common in thick grass (chalk) as it was found to be in codominant grass and heather (Greensand).

Woodlark. Sparse or patchy ground vegetation with a song post—chalk and Greensand.

Meadow pipit. Thick ground vegetation for nesting—chalk and Greensand. There were seven pairs to the mile on the thick grass of type 1 (chalk), but only one pair in 13 miles of sparse grass. On Greensand, all the 86 territories analysed were in phase 4.

Goldcrest. In the best stands of evergreen scrub—chalk and Greensand.

Coal tit. As the last, but none seen in open yew.

Whitethroat. A scrub species requiring thick lower vegetation for nesting—chalk and Greensand. This stand was most typical of type 10, and here the whitethroat was most numerous with eight pairs to the mile. The figures show a marked avoidance of evergreen scrub.

Willow warbler. Bush or tree for song post, and ground vegetation for nesting—chalk and Greensand. Nine pairs to the mile in seven miles of chalk thorn scrub, four pairs to the mile in six miles of Greensand pine and gorse scrub, all having good or moderate ground vegetation, but only one pair to the mile in seven miles of chalk yew scrub with its sparse undergrowth.

Blackbird. Well distributed throughout all chalk scrub. Two pairs in the gorse scrub on Greensand but none in the pine scrub.[1] Two pairs were seen in 13 miles of grass with occasional bushes.

Wheatear. Both on chalk and Greensand the limiting factors were sparse or absent ground vegetation, and a rabbit hole for nesting. Of the twenty pairs seen during the chalk down walks, all were on sparse grass types (see discussion in Venables, 1937, p. 84).

Dunnock. In all the scrub types, chalk and Greensand, except the very open juniper scrub.

Wren. Thinly distributed throughout the denser scrub—chalk and Greensand. The two thinnest types (chalk open juniper and Greensand pine) being avoided.

Cuckoo. More or less evenly distributed where it could get a good look-out place and

[1] After this was written, a breeding pair was found in Greensand pine scrub.

where there were plentiful nests of small Passerines—chalk and Greensand. Dense, closed scrub was avoided.

Kestrel. Tree for nesting on Greensand, substituted by tall scrub on chalk.

Stock dove. A hole-nester, tree or ground, on Greensand. Only one pair seen during the chalk counts; presumably nesting in a rabbit hole.

Pheasant, red-legged partridge and common partridge. The habitats on Greensand were analysed by the finding of nests or by some sound indication that the nests were there. They were all on phase 4 with its dense ground vegetation for concealing eggs. During the walks across chalk downland no nests of these species were found; the birds recorded in Table 2 being the non-incubating ones scattered over various types. The "woodland" species (the pheasant) was usually in scrubland, and the partridges mostly on open grassland.

The only markedly dissimilar species, common to both formations, was the *lapwing.* On both chalk and Greensand, sparse (also absent in the case of the latter) ground vegetation was chosen for nesting. On Greensand one pair was found on phase 3, twelve on phase 2 and nineteen on phase 1. On chalk, fifty-eight pairs were found in 13 miles of sparse grass, and only one pair on six miles of thick grass. On Greensand, however, they were all found breeding not far from marsh or water while on the chalk they were, of necessity, up in the high, dry hills.

It will be seen how closely the birds common both to Greensand heaths and chalk downland have parallel habitats on both formations. Thick grass is used instead of the rich heather growth, and sparse grass instead of the poor ground vegetation found for the first few years after a heath fire. The gorse patches and thickets of young pine on heathland are used successfully in place of the deciduous and evergreen scrub stands on the chalk hills. Nevertheless, these differences in flora would seem to be of some importance, as a number of species are found on one or other of the formations but not on both.

(Compare Table 2 in the present communication with Table 2 in Venables, 1937.)

4. Summary

1. The distribution of breeding birds (determined by walking counts) on the chalk hills known as the South Downs is described, and compared with that of Surrey Lower Greensand heaths.

2. The plant associations on the chalk downs are divided into eight main types; three of grass, two of deciduous scrub, and three of evergreen scrub.

3. There is a short general discussion on the bird distribution, followed by a more detailed one on the grass types and then on the scrub types. The complete data are given in Table 2.

4. The general succession of the ground vegetation on the Greensand heaths is compared, so far as possible, with the grass types on the chalk. The two main Greensand heath scrub formations are described for the purpose of comparison with those on chalk. The species of birds occurring on both places are discussed individually.

5. As far as practicable with the different flora, the birds are found to choose much the same habitats both on chalk hills and on Greensand heaths.

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Appendix

Plant names used in the text

Beech	*Fagus sylvatica*	Heather	*Calluna vulgaris* and *Erica cinerea*
Birch	*Betula* sp.	Juniper	*Juniperus communis*
Bracken	*Pteridium aquilina*	Oak	*Quercus* sp.
Bramble	*Rubus* sp.	Pine	*Pinus* sp. (mainly *sylvestris*)
Elder	*Sambucus nigra*	Sloe (Blackthorn)	*Prunus spinosa*
Gorse	*Ulex europaeus*	Yew	*Taxus baccata*
Hawthorn	*Crataegus oxyacantha*		

THE ANALYSIS OF AN ANIMAL POPULATION

By C. H. N. JACKSON

(*With* 1 *Figure in the Text*)

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1. Introduction

In a previous paper (Jackson, 1936) an account was given of the estimation of a tsetse-fly population through the year by means of the "Lincoln Index". Since then certain amendments have become necessary as the mathematical treatment has improved, and the method has been extended to provide estimates of rates of birth, death and dispersal which were previously unobtainable. It is the purpose of this paper to explain and describe these improvements and extensions, as the use of the method seems potentially of wide application in problems of animal ecology.

The principle is simple. A random sample of individuals is marked: at some later time a random sample is caught and examined: either the initial marking or the later catching is done evenly over the area selected for study. The second catch includes a certain proportion of individuals recognized by their marks as having been caught in the first sample. Then, subject to conditions considered below, the proportion of recaptures to total taken in the second catch ought to be the same as the proportion initially marked to the total population. That is, the population is equal to

$$\frac{\text{total marked} \times \text{total caught when recapturing}}{\text{recaptures}}.$$

For closed areas, this formula gives good results when the breeding and non-breeding seasons are well defined and when neither is overlapped by the interval between marking and recapturing. For other conditions modification is necessary.

One assumption and some general principles must be stated. The assumption is that no individuals dealt with in an experiment must be any more likely than any others of the species to show themselves to the catchers on

the recapture day. Thus if one sex or one age group of the animals is more willing to appear and be caught, that sex or group must be separately considered throughout. When the activity of the animals determines their readiness to be caught, and when individuals overlap each other in their activity periods, marking or recapturing must be continued long enough, or the interval between them must be made long enough, to damp out the effect of periodic individual activity. For example, if an individual animal is likely to be active about every second day, those marked on any one day are either more or less likely than those unmarked to be seen on the day following. To counteract this, we must either mark on two consecutive days and recapture later, or mark all on one day and recapture on two days, or after many.

Whenever, as must often be necessary, the interval between marking and recapturing is not negligibly short, the formula must be modified to deal with animals whose generations overlap or which, between marking and recapturing, move into or out of the area selected for study. This is because the proportion of marked to unmarked individuals will diminish between marking and recapturing through death or emigration of some of the marked individuals, and their replacement by others being born or hatched, or entering the area from outside.

But if the environmental conditions are not exceedingly inconstant, the proportion of marked to unmarked individuals will decrease in a fairly regular way (actually in geometrical progression) with the passage of time after the marking date: and by taking samples at regular intervals after marking we can estimate the rate of decrease of the marked proportion. Once this is known, we are able to estimate what the proportion was on the date of marking, and so apply the formula already given. Even with a relatively inconstant environment, a smooth "die-away" curve can be obtained by taking averages of single curves, and reliable estimations of the population can be made.

2. Estimation of the population

The data here considered are drawn from studies in Africa on the tsetse-fly *Glossina morsitans* Westwood, and refer only to males which had had their first feed and were therefore not recognizably young. The marking area was a square with sides 4 miles long; and for the purpose of estimating dispersal rate (see below) it was subdivided into quarters each of 4 sq. miles. The flies were marked at weekly intervals, actually on the first 3 days of every week, evenly throughout the square, the four marking parties avoiding any definite paths. The marking was altered weekly, and every quarter-square was distinguished by a separate mark.

The method has already been explained (1936) but must be recalled to assist the understanding of subsequent sections of this paper. The number of individuals caught and marked at regular intervals will probably vary from

date to date. The first step, therefore, is to correct the recaptures as if some constant number (say 100) had been marked, and the same number caught on every recapture date. For example:

Marked	Caught on recapture dates					
1582	1547	1307	603	1081	1261	1798
	Recaptures					
	103	82	24	31	10	11

The first corrected figure (y_1) will be $\frac{103 \times 100 \times 100}{1582 \times 1547}$, the second ($y_2$) will be $\frac{82 \times 100 \times 100}{1582 \times 1307}$, and so on. When all six have been corrected in this way, they become:

y_1	y_2	y_3	y_4	y_5	y_6
0·4207	0·3966	0·2574	0·1812	0·0501	0·0387

What we require to find from the above series is y_0, which we will call a, the corrected figure which would have been obtained had we been able to recapture on the date of marking. For this purpose, we must first find r, the common or average ratio of each value of y to the value preceding it, or of y_1 to a. For general purposes r can be calculated from the formula

$$r = \frac{y_2 + \ldots + y_k}{y_1 + \ldots + y_{k-1}}.$$

But Mr W. L. Stevens has lately shown that when, as in our example, $k = 6$, a more accurate estimate is:

$$r = \sqrt{\frac{y_3 + y_4 + y_5 + y_6}{y_1 + y_2 + y_3 + y_4}},$$

which in the example given works out to 0·6480. To find a we calculate

$$a = \frac{y_1 + \ldots + y_{k-1}}{r} - (y_1 + \ldots + y_{k-2}),$$

which for this example

$$= \frac{y_1 + \ldots + y_5}{r} - (y_1 + \ldots + y_4)$$

$$= 0{\cdot}759.$$

Now since all the values of y, and therefore that of a, have been corrected as if 100 were marked and 100 caught on every recapture date, and since the population formula is (see above)

$$\frac{\text{total marked} \times \text{total caught when recapturing}}{\text{recaptures}},$$

the population in the present instance will clearly be

$$\frac{100 \times 100}{a} = 13{,}200 \text{ approximately.}$$

To summarize this calculation:

(i) Correct all the recaptures as if 100 had been marked initially and 100 caught on all recapture dates.

(ii) Take the sum of all but the first two.

(iii) Divide by the sum of all but the last two.

(iv) Take the square root, thus finding r.

[1](v) Take the sum of all but the last one.

[1](vi) Divide by r.

[1](vii) Subtract the sum of all but the last two, to find a.

(viii) Divide into 10,000 to get the population.

Average estimates of population on several recapture dates may be made either by averaging the respective values of y_1, and y_2, etc., and calculating a from the result, or by averaging values of a calculated from separate recapture curves. The alternative method given on pp. 853–4 of the paper quoted above is more troublesome and seems to be less accurate, not more accurate as there stated.

3. The "negative" method

This also was described in 1936 (p. 854). In the "positive" treatment exemplified in the last section, we considered recaptures in subsequent catches of flies marked on a certain date. We can equally well consider recaptures on a certain date from flies marked in previous catches. This treatment I have called the "negative" method (Fig. 1). Both methods ought to give nearly the same value of a for any particular date. For example:

Caught	Marked on previous dates					
1558	1183	1198	1401	1299	1086	1262
	Recaptures					
	70	48	28	17	5	1
	Corrected recapture figures					
	0·3798	0·2569	0·1283	0·0840	0·0296	0·0051

Proceeding exactly as before, we find r to be 0·5394, from which we calculate $a = 0·780$, which divided into 10,000 gives a population estimate of about 12,800.

These two examples are drawn from actual field data, and refer to the same date. It will be seen that the two population estimates, 13,200 and 12,800, are not very discrepant. (It will be observed that the number "caught" in the second example is lower than the number "marked" in the first, whereas they should normally be equal. This is because 24 individuals, being still recognizably young when marked, were admissible as flies "marked" but not as flies "caught": any recovered a week later would have had their first meal, and would therefore be normal mature male flies.)

[1] Or, take the sum of all, divide by r, and subtract the sum of all but the last one.

4. Death-and-emigration and birth-and-immigration

We may use r_+ for the common ratio found by the "positive" method, and r_- for the common ratio by the "negative" method. Also, let

$$P = \text{population} = \frac{10{,}000}{a},$$

$D+E$ = death-and-emigration rate,

$B+I$ = birth-and-immigration rate,

n = the date for which the population is worked, by the "positive" method.

By "survival" is meant survival of flies still living in the marking area.

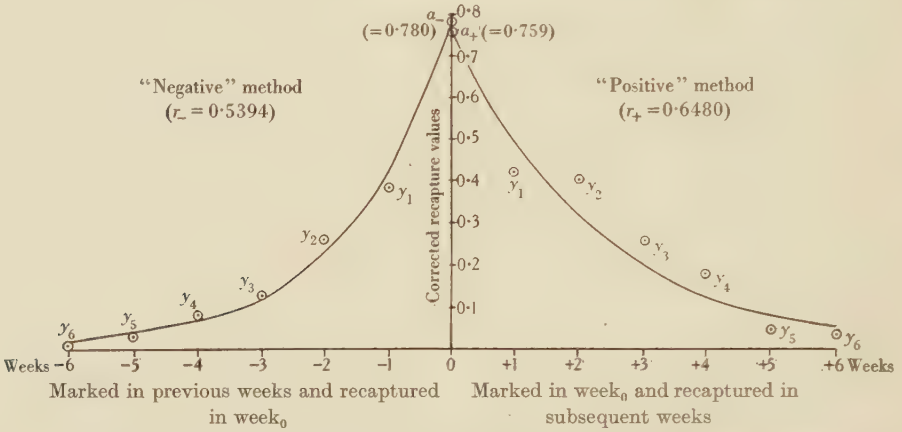

Fig. 1. Illustration of the calculation of the extrapolated points (a) by the "positive" and "negative" methods. All values are taken from the example in the text. The agreement between a_+ and a_- is not usually so close as in this example.

Of flies marked on any date, n, and recaptured on the following date of catching, $n+1$, the survival rate per fly if the whole population were seen on the recapture date would be the actual, uncorrected recaptures divided by the number marked. But we do not see the whole population, P_{n+1}, on the date$_{n+1}$, and the actual survival rate is

$$\frac{\text{recaptures}}{\text{number marked}} \times \frac{P_{n+1}}{\text{number caught date}_{n+1}}.$$

Since the corrected recapture figures, y, are those which should have been obtained had 100 been marked or caught on every date, we can write the above expression equal to

$$\frac{(y_1)_n}{100}\,\frac{P_{n+1}}{100}$$

$$= \frac{(y_1)_n}{a_{n+1}}.$$

This being the survival rate per fly, the death-and-emigration rate per fly is

$$D+E=1-\frac{(y_1)_n}{a_{n+1}},$$

which for smooth curves is the same as

$$1-r_-,$$

where r_- is r_- calculated for the date $n+1$.

To find the birth-and-immigration rate we argue as follows:

From date_n to date_{n+1} there die or leave the area

$$P_n(1-r_-).$$

Therefore there remain in the area from date_n

$$P_n-P_n(1-r_-).$$

Therefore there enter, or are hatched or born

$$P_{n+1}-[P_n-P_n(1-r_-)]$$

$$=\left[1-\left(\frac{P_n}{P_{n+1}}r_-\right)\right](P_{n+1})$$

which is a rate per fly of

$$B+I=1-\left(\frac{P_n}{P_{n+1}}r_-\right)$$

$$=1-\left(\frac{a_{n+1}}{a_n}r_-\right)$$

which for smooth curves is the same thing as

$$1-\left(\frac{a_{n+1}}{a_n}\frac{(y_1)_n}{a_{n+1}}\right)$$

$$=1-\frac{(y_1)_n}{a_n}$$

$$=1-r_+.$$

We have seen that the death-and-emigration rate per fly is $1-r_-$, and the birth-and-immigration rate is $1-r_+$. The dates to which these estimates refer, however, are not the same as the date for which the population was calculated, but are removed from it by a time equal to the mean interval between marking and recapture of all the recaptured flies used in the estimation of r. When r is about 0·6, as in the example given above, this time is between $1\frac{1}{2}$ and 2 intervals from the date for which the population was estimated.

In that example, the values of r by the "positive" method and by the "negative" method respectively were 0·6480 and 0·5394. The birth-and-immigration rate is therefore 0·3520 and the death-and-emigration rate is 0·4606. These values refer respectively to from $1\frac{1}{2}$ to 2 intervals (dates) after and before the date for which the population was calculated.

of the idea of the "Lincoln Index", and makes allowance for the factors of birth, death, and migration onto and off the area studied. It is illustrated by field data obtained from tsetse fly populations in East Africa.

8. Acknowledgements

I am very grateful to Prof. R. A. Fisher, F.R.S., and to Mr W. L. Stevens, of the Galton Laboratory, London, for their interest and invaluable help at all stages of this work.

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CANADIAN ARCTIC WILD LIFE ENQUIRY, 1937–38[1]

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(*With 4 Figures in the Text*)

1. Introduction

This is the third annual report on replies to zoological questionnaires sent out by the Northwest Territories Administration, Ottawa, and by the Hudson's Bay Company. The forms ask for opinions on the abundance of certain animals during one year ending 31 May compared with the one before it. The government form is concerned with lemmings (*Lemmus* and *Dicrostonyx*), the arctic fox (*Alopex lagopus*), snowy owl (*Nyctea nyctea*) and ptarmigan (*Lagopus*) and with disease in sledge dogs. The Company's form goes to posts outside the Arctic as well, and, with the exception of ptarmigan, covers these animals and certain others. The object of the enquiry is to maintain a current record of some of those changes in animal numbers which are such a remarkable feature of the Arctic. It is hoped to define the years and the areas in which these fluctuations occur and to compare the different variables.

Sledge dogs are subject to various diseases, some of them perhaps contracted from wild animals such as the arctic fox. For this reason reports on the health of sledge dogs are being studied together with the cycle in Arctic wild life; and conditions further south are being followed for comparison.

There were 35 replies to questionnaires sent out by the Northwest Territories Administration. This material has been collected and forwarded for analysis in the Bureau of Animal Population through the good offices of the Commissioner of the Northwest Territories, Dr Charles Camsell, and the Deputy Commissioner, Mr R. A. Gibson. 70 reports were received from Hudson's Bay Company posts in the Arctic and Subarctic, and other posts supplied information on sledge dogs. The Fur Trade Commissioner in Winnipeg, Mr Ralph Parsons, and his staff, with the permission of the Governor and Committee of the Hudson's Bay Company, have kindly placed these annual zoological reports at the disposal of the investigation.

2. Methods

The data from each year's enquiry are condensed and reproduced as far as possible without distortion of the original replies, and irrespective of their apparent merit. The reader is thus in possession of all the information on

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

which the report is based and may see both the possibilities and limitations of the questionnaire method.

In Table 1 are given the opinions of observers about comparative and absolute abundance of arctic foxes, lemmings, "mice" and snowy owls. (The data on ptarmigan are being reserved.) These replies are arranged in a general order east to west or south to north and are divided into a number of rather arbitrary groups. Table 2 shows for each species (except "mice") how opinions as to their relative abundance are distributed within these groups.

The areas described in Table 1 have been plotted on a map from which Figs. 1, 3 and 4 have been constructed. All the areas reporting *increase* have been covered with arrows pointing up, these being spaced out, where a pattern can be made, at half-inch intervals on a map of 100 miles to an inch. Similarly the areas reporting *decrease* or *no change* have been indicated by arrows pointing down or horizontally. These symbols translate into diagrammatic form the comparisons listed in Table 1. They also (1) provide a means of making a very rough estimate of the percentage area covered by each kind of reply (i.e. one arrow $\doteqdot$ 2500 sq. miles), and (2) show where there is disagreement. A method of expressing these two aspects was evolved and explained in the first two reports, and the figures were found to agree remarkably well with those compiled from the number of observers. In view of this, and of the approximations involved in the area method (at any rate under the particular conditions of this enquiry) it is now felt that not much additional information is obtained by counting the arrows.

The previous reports should be consulted for a discussion of the species and of method. Some of the details with additional notes are given here:

(1) *Areas.* The wild life enquiry is confined to the groups described in Table 1 and does not include the Mackenzie River valley or, in the case of lemmings, group 3, and the south parts of groups 1 and 10. Areas are mapped as described, except where, as indicated by square brackets in Table 1, places were not located or the area seemed too far outside the breeding or migratory range of a species. A difficulty in this connexion is that observers often describe only one area for several species without indicating to what part of it some of them are limited. In these cases the area is listed in Table 1 as described, but not always mapped in full. As a rule, however, the replies are accepted without corrections.

(2) "*Mice.*" This column in Table 1 is given to supplement the information on lemmings, as the various species of wild mice and voles are also of importance as food for predators. The data are not at present used in the analysis, but it should be realized that there is likely to have been confusion among some observers in distinguishing between lemmings and "mice".

(3) *Count of observers.* There are three difficulties in making Table 2. Observers may (*a*) give different opinions for different parts of their area, or (*b*) times of the year, or (*c*) describe an area overlapping more than one of the arbitrary groups. With (*a*) the vote is divided; with (*b*) the opinion given for the year as a whole is counted: events at particular times are simply listed in Table 1; with (*c*) an observer's vote is counted only in the one group containing either his headquarters or the largest portion of the area.

(4) *Fort McKenzie.* This report is listed in group 2 but not included in the totals. It may

Table 1. *Summary of original data on arctic fox, lemming, snowy owl and sledge dog (part) for* 1937–38

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, × = not noticeably scarce or abundant, a. = abundant, v. = very.

Sledge dogs: 0 indicates a report that disease was entirely absent. 0* = report of disease in minor proportions, + = more serious disease; details in Table 3 (*a*). One symbol is given each observer except where indicated (2), etc.

Square brackets indicate observations that have been partly or entirely omitted from either the map or the calculations—see text for explanation.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

	Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
Group 1. Northern Labrador coast					
Frenchman's Island, outside islands and 20 miles inland	D. s.	[I. a.]	I. a.	I. a.	0
Cartwright and 50 miles radius	I. s.	—	I. a.	I. a.	0
Rigolet, south 50, north 75, west 35 miles	I. s.	I. s.	I. ×	I. ×	—
Northwest River [and inland 400 miles, by trappers' reports]	I.	—	I.	—	—
Makkovik, 30 miles north and south [and inland, north-west, 100 miles from coast]	I. ×	—	I. ×	I. a.	0
Hopedale and 30 miles radius	I. ×	—	I. a.	I. ×	0
Davis Inlet and 30 miles radius	I. ×	—	I. a.	I. ×	0
Voisey's Bay, north-east 108, north 85, north-west and south-west 40 miles	I. a.	I. a.	I. a.	I. ×	—
Nain, 35 miles radius and north-west 70 miles	I. ×	I. a.	I. a.	I. ×	—
Nutak	I. ×	I. ×	I. a.	N. ×	0
Hebron and from Sedlik Bay to Napartok Bay	I. ×	I. v.s.	I. v.s.	I. a.	0
Spring	—	v.a.	v.a.	—	—
Port Burwell, Killinek Island and mainland within 100 miles	I. s.	I. a.	D. s.	I. a.	0*
Group 2. Coast of Northern Quebec, south to Richmond Gulf and inland					
Georges River and 50 [to 150] miles radius	I. v.s.	I. v.a.	I. v.a.	I.	—
Whale River to Georges River	I. s.	I. a.	I. a.	I. s.	—
Georges River, inland, *April*	v.a.	—	—	—	—
Fort Chimo and 25 miles radius	I. ×	I. ×	D. v.s.	I. ×	—
[Fort McKenzie and 120 miles radius]	[I. v.s.]	[D. v.s.]	[D. s.]	—	—
Leaf River, Leaf Bay and coastal area 40 miles east	—	I. a.	I. v.a.	I. ×	—
Early winter	D. ×	—	—	—	—
Payne Bay to Payne Lake; south 25, north 35 miles	D. ×	I. ×	—	D. s.	—
Fall	a.	—	—	—	—
Diana Bay: from Cape Hopes Advance in the north to within 30 miles of the Payne River in the south; west to a line from Burgoyne Bay to the Payne River	D.	D. s.	D. v.s.	D. ×	—
After Christmas	v.s.	—	—	—	—
Stupart Bay to East Sugluk and Burgoyne Bay	v.s.	I. v.a.	D. v.s.	D. v.s.	—
Sugluk West and 80 miles radius	I.	I.	—	I.	—
Late spring	v.a.	v.a.	—	v.a.	—
Wolstenholme; east to within 20 miles of Sugluk, south 72 miles to Kovik River	I. v.a.	I. v.a.	I. v.a.	D. v.s.	—
Spring	[D.]	—	—	—	—

Table I (*continued*)

		Arctic fox	Lemming ["Mice"]		Snowy owl	Sledge dog
	Cape Smith, inland 50, south 20 and north 70 miles	I. a.	I. ×	—	I. ×	—
	January–May	[D.] ×	—	—	—	—
	Povungnetuk and 40 miles radius	I. a.	I. s.	I. a.	—	—
	Port Harrison, north to Koklak River, south to Nastapoka River	I. ×	I. ×	I. ×	I. ×	—
28.	Port Harrison, and from Kogatuk Bay to Broughton Island	I.	I. ×	—	D. ×	0
	Middle of November–May	—	—	—	v.s.	—
	Group 3. South parts of Hudson Bay, James Bay and inland					
	Belcher Islands	I. s.	[D. s.]	—	I. a.	0
	Spring	—	—	—	[D.] s.	—
	Great Whale River north to Richmond Gulf, south to Cape Jones	I. a.	[I. a.]	I. a.	D. s.	–
	Fort George and 100 miles radius	I. ×	[N.]	—	v.s.	—
	Kanaapuscow, north and south 100; east [250] miles, west to coast	I. ×	[D. ×]	N. ×	N. ×	—
	Eastmain, north 60, south 20, inland 150 miles	I. s.	—	I. a.	I. s.	—
	Neoskweskau and 50 miles radius; [Nitchequon and 50 miles radius]	I. s.	—	I. ×	—	—
	Albany	—	—	I. a.	—	–
	November	—	—	D.	—	–
	Kapisko north to Lawashi River, south 6 miles along coast, inland 6 miles along Kapisko River	—	—	I. a.	N. ×	0
	Attawapiskat, south to the Lawashi River, 150 miles inland, north to Cape Henrietta Maria. Also Agamiski Island	D. s.	—	I. v.a.	N. ×	0
	Lake River to 30 miles south of North Lawashi River, as far inland on all rivers as Opinega Lake and north to Trout River	N. ×	—	N. a.	N. ×	—
	Weenusk, along the coast north 100, south 50 and inland [200] miles	I. ×	—	I. a.	N. ×	—
	Severn, along the coast north-east to Kaskatamagan, south-east to Weenusk and inland [half-way to Trout Lake]	I. ×	—	D. s.	D. s.	0
	York Factory, north 100 miles, east to Kaskatamagan, inland [almost to Shamattawa]	I. ×	—	N. ×	N. ×	–
	Group 4. West coast of Hudson Bay, north from Nelson River					
	Churchill, Seal River, North River, and along coast	I. ×	D. v.s.	D. v.s.	N. ×	—
	Caribou; from Seal River to Big River (north and south 70 miles); east 40 and west 30 miles	I. a.	—	I.	D. s.	0
	Nonala and 50 miles radius	D. ×	D. ×	D. ×	D. ×	—
	Early fall. On the sea ice *in March*	v.a.	—	—	—	—
15.	Lat. 59°–61°. Long. 97°–102°	D.	I.	—	D. v.s.	0
20.	Lat. 60°–61° and from Nueltin Lake to within 50 miles of Hudson Bay coast	I. s.	D. v.s.	—	N. s.	0
	Nueltin Lake to Ennadai Lake	N.	—	D. s.	N.	0
	Winter	—	D. s.	—	—	—
	Eskimo Point, west to edge of bush, north to Maguse River, south to Big River	N. ×	D. ×	D. ×	D. ×	0
	North-west of post	I.	—	—	—	—
	South of post. On coast *until late spring*	s.	—	—	—	—

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
12.	Eskimo Point	N.	N.	—	N.	0
	Padley and 8 miles radius	I. ×	D. ×	D. ×	—	0
	Tavane and 30 miles radius	I. a.	N. ×	I. a.	N. ×	0
	On coast edge	v.s.	—	—	—	—
	Chesterfield to Cape Fullerton; south to Rankin Inlet and 100 miles inland	I.	D. s.	—	D. s.	0
	Baker Lake, Beverly Lake and Kazan River (Group 4); Back River (Group 9)	I. ×	N. ×	—	D. s.	0
	Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
	Repulse Bay, north-west to Committee Bay, east at Lyon Inlet, north at Igloolik and its vicinity on Melville Peninsula	I. a.	I. a.	—	—	0
	Spring	—	[D.] v.s.	—	—	—
	Southampton Island (whole island)	I. ×	I. ×	N. ×	N. ×	—
	Group 6. Southern Baffin Island					
	Lake Harbour east to Gabriel Strait, west to Fair Ness	I. ×	I. ×	—	I. ×	—
	Winter	—	[D.] v.s.	—	v.s.	—
32.	Lake Harbour district and south coast from Frobisher Bay to Foxe Channel	I.	I. ×	—	D. v.s.	0*
	Late spring	—	[D.] v.s.	—	—	—
	Cape Dorset and Foxe Peninsula	I.	I. ×	—	D. s.	—
	Frobisher Bay (post) and from Cape Haven round the bay to Newell Sound	I. ×	I. ×	—	D. s.	—
	February–March	[D.] v.s.	—	—	—	—
30.	Pangnirtung: mainly coastal observations in Cumberland Sound, Hoare Bay and due north on Davis Strait	I. ×	I. ×	—	I. ×	—
	Pangnirtung Fjord, Cumberland Sound and south to north shore of Frobisher Bay	I. ×	I. ×	—	N.	0
	Group 7. Northern Baffin Island and north					
	Clyde River to Coutts Inlet and Home Bay	I. ×	I. ×	—	I. ×	0*
	Early fall	v.a.	—	—	—	—
31.	Pond's Inlet, south to Home Bay, south-west to Igloolik, north to Lancaster Sound; south shore Bylot Island	I. a.	N. v.a.	—	I. v.a.	0
	Spring	—	[D.]	—	—	—
	Pond's Inlet, Eclipse Sound and Navy Board Inlet	I. ×	D. ×	—	D. ×	—
	Arctic Bay to Elwin Inlet and end of Admiralty Inlet	—	—	—	D. s.	—
	As above and Agu Bay	I. v.a.	—	—	—	—
33.	Craig Harbour, Ellesmere Island	I. ×	N. v.s.	—	—	0
	Group 8. Boothia Peninsula and islands west and north					
	Fort Ross, Boothia Peninsula and Somerset Island	I. ×	I. ×	—	—	—
	King William Island (Group 8), Adelaide Peninsula and east to Pelly Bay (Group 9)	I. v.a.	N.	—	I. v.a.	0
	Cambridge Bay to Wellington Bay, and Albert Edward Bay (Group 8); Coast of Kent peninsula on Dease Straits (Group 9)	I. ×	I. a.	—	—	0

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge Dog
35.	Cambridge Bay west to Wellington Bay, east to King William Island taking in shores of all islands (Group 8); White Bear Point to Cape Alexander (Group 9)	I. ×	I. v.a.	—	v.s.	—
	West of Cambridge Bay to Wellington Bay and Perry River to [Gjoahaven], King William Island	—	-	—	—	0
	Reid Island to Lady Franklin Point and to north shore of Prince Albert Sound	I. ×	I. v.a.	—	I. ×	—
19.	Minto Inlet	v.s.	v.s.	—	D. v.s.	0
	May	a.	[I.] v.a.	—	—	—
	Fort Collinson and east and west shore of Prince of Wales Strait	D. ×	I. ×	—	N. ×	—
	Group 9. Pelly Bay, west to east of Coppermine River, and inland to Back River					
	Bathurst Inlet: west coast from Wollaston Point south to Western River and inland 100 miles; east coast from Gordon Bay to Western River and inland 50 miles. Also Lakes Finnie and Beechey	N. ×	N. ×	I. ×	—	0
8.	100 miles south of East Kugaryuak River (roughly 10 miles east of White Sandy River)	v.s.	—	—	—	0
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
	Stony Rapids, 150 miles north of ...	—	[I. ×]	N. ×	D.	—
	April (especially)	I. ×	—	—	—	—
	Snowdrift and between Lat. 61°–64° and Long. 106°–112°	N. s.	N. ×	N. ×	D. s.	0
	East of Long. 107° *in spring*	[I.]	—	—	—	—
5.	Fort Reliance	—	N.	—	—	0*
	Fort Resolution and 40 miles radius ...	I. ×	—	N. ×	—	0
2.	Ptarmigan Lake, Clinton Colden Lake	I. ×	I. ×	—	N. s.	0
	Fort Reliance	—	—	—	—	0
6.	Lac de Gras, south to Outram Lakes ...	D. v.s.	N. s.	—	N. s.	0
29.	Headwaters of Coppermine, Lakes Providence and de Gras	N. v.s.	I. v.a.	—	N. s.	0
23.	Yellowknife mining district	—	D. s.	D.	I. s.	0
	Fort Rae, south-east 80 miles to Yellowknife River [north-west 150 miles to end of Lac La Marte, north-north-west 180 miles to Lake Grandin], approx. north 150 miles to Lake Hardisty and 150 miles north-east to end of Snare Lake	N. s.	I. a.	I. a.	—	0
	Group 11. Coppermine River to Alaska					
21.	Coppermine Settlement and 12 miles up river to Bloody Falls	N. v.s.	N. v.s.	—	N. v.s.	0
18.	Dismal Lakes District	I.	I.	—	I.	0
16.	North-east shore of Great Bear Lake ...	—	I. v.a.	—	—	0
25.	From Cape Krusenstern 50 miles west and south to Rae River	I. ×	N.	I.	I. v.a.	—
	Krusenstern and Basil Bay; also Lady Franklin Point	—	—	—	—	0 (2)
34.	South shore of Beaufort Sea between Long. 122° and 133°	I. ×	D. ×	—	D. ×	0
	Baillie Island, south-east 60, south 70 miles	I. ×	I. a.	—	I. a.	—
	Spring	v.s.	[D.]	—	—	—

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
3.	Mackenzie Delta and coast between Herschel and Baillie Islands	N. ×	I. v.a.	—	I. ×	—
	Forts Norman, Good Hope and McPherson; Aklavik	—	—	—	—	+ (4)
	Tuktuk, south to south of Kittigazuit, east to Kugalook, north to Cape Dalhousie, west to Richards Island ...	D. ×	—	I. a.	—	0
22.	Mackenzie R. delta, East Branch, and Richards Island	D. v.s.	I. v.a.	—	–	—
	As above and east to Eskimo Lakes ...	—	v.a.	—	D. v.s.	—
	Aklavik to [Point Separation and] Shingle Point	D. s.	D. ×	D. ×	D. ×	+
	Shingle Point to Demarcation Point, about 130 miles	D.	N. ×	—	—	0

be regarded as a subdivision of group 2 subject to rather different conditions from those on the coast.

(5) *Sledge dog.* Only one symbol is placed on the map (Fig. 2) for each area, except where two or more distinct places are named. A circle (at the centre or headquarters of the area) indicates a report of disease absent or in very minor proportions; a plus sign is given where more serious disease or an epidemic was reported. Absence of disease (or of sledge dogs) may also be inferred at the Hudson's Bay Company posts in Table 1 from which no statements were received; though these posts are not distinguished on the map.

3. RESULTS

By 1935–36 decrease to great scarcity had occurred among all species. In the following year conditions improved in the Eastern Arctic, particularly on the north coast of Quebec and in Baffin Island. In the Western Arctic little recovery was apparent. In 1937–38 lemmings and snowy owls increased on the coast of the Quebec peninsula and in parts of the Western Arctic, but started to decrease in Baffin Island. Recovery continued among arctic foxes in the east and started on the islands and parts of the coast further west.

Lemming. From Rigolet in Labrador round the coast of the Quebec Peninsula to Port Harrison in Hudson Bay, lemming reports were of increase at all places except Diana Bay. (There seems also to have been a considerable increase among "mice".) Reports of increase on this coast have risen from 3 out of 15 (1935–36) through 10 out of 19 (1936–37) to 18 out of 19 (1937–38). On the west coast of Hudson Bay about half the observers in both 1935–36 and 1936–37 thought that lemmings were increasing; but during 1937–38 only 1 out of 11 held this view. From Repulse Bay, Southampton Island and all of southern Baffin Island increase was reported; but in the Repulse Bay and Lake Harbour districts there were reports of decrease in the latter half of the period, and a similar report came from Northern Baffin Island.

In the Western Arctic there seems to have been an improvement in lemming numbers on Boothia Peninsula, Somerset Island, Victoria Island and from

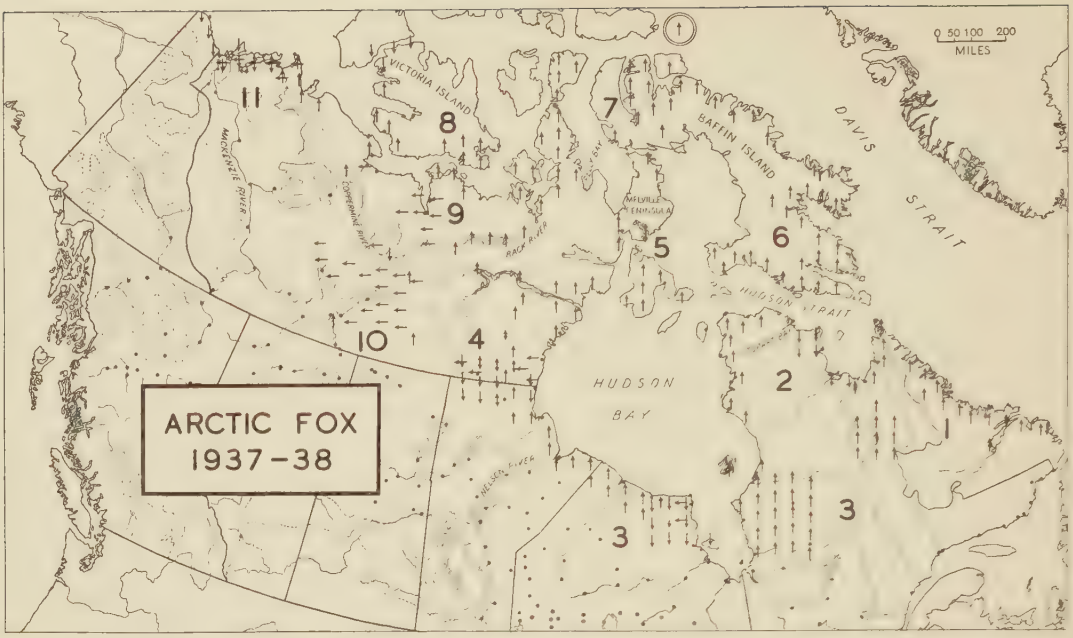

Fig. 1. State of the arctic fox population in 1937–38 compared with 1936–37. Arrows indicate the areas covered by observers reporting Increase (↑), Decrease (↓), and No change, not abundant (←). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset Craig Harbour, Ellesmere Island.

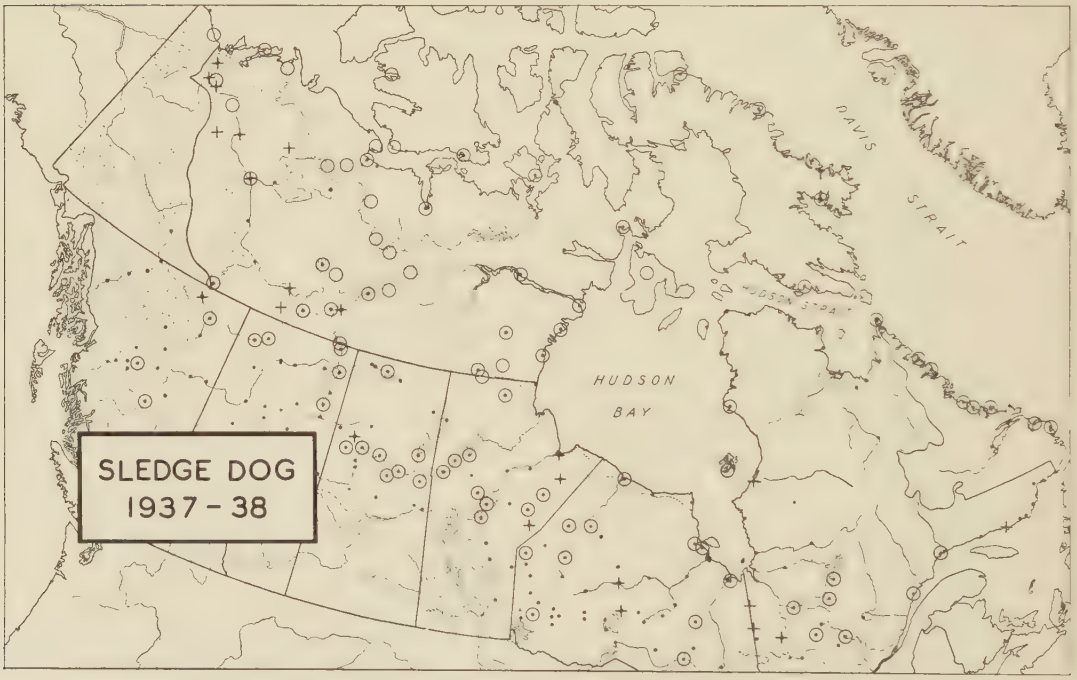

Fig. 2. Prevalence of disease among sledge dogs in 1937–38. Reports of disease are indicated +; disease absent or in minor proportions 0. Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.

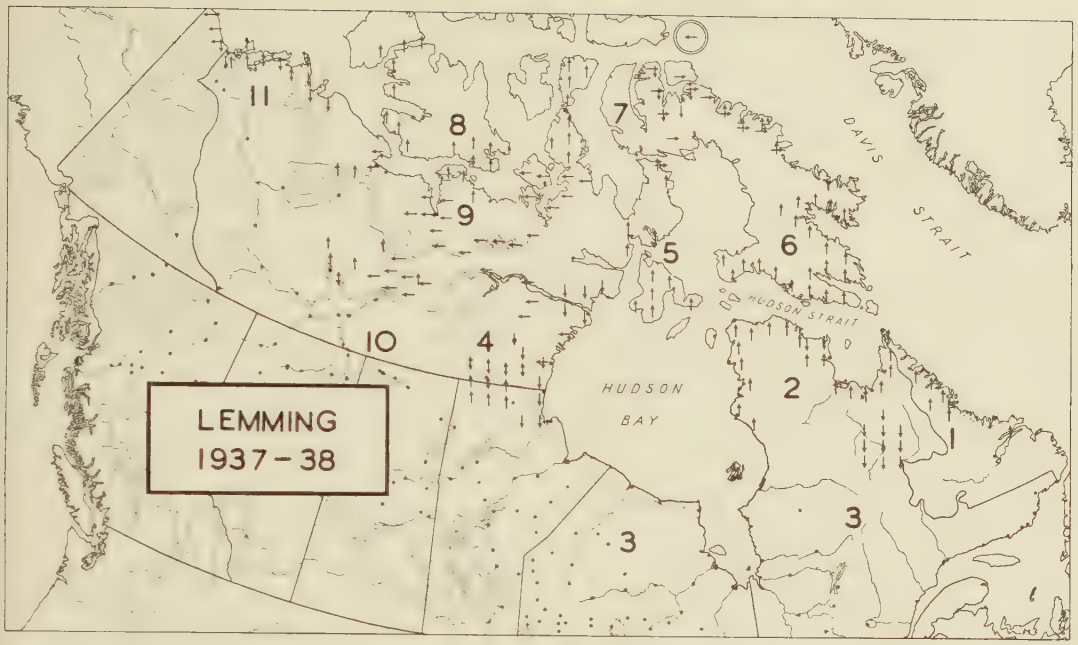

Fig. 3.

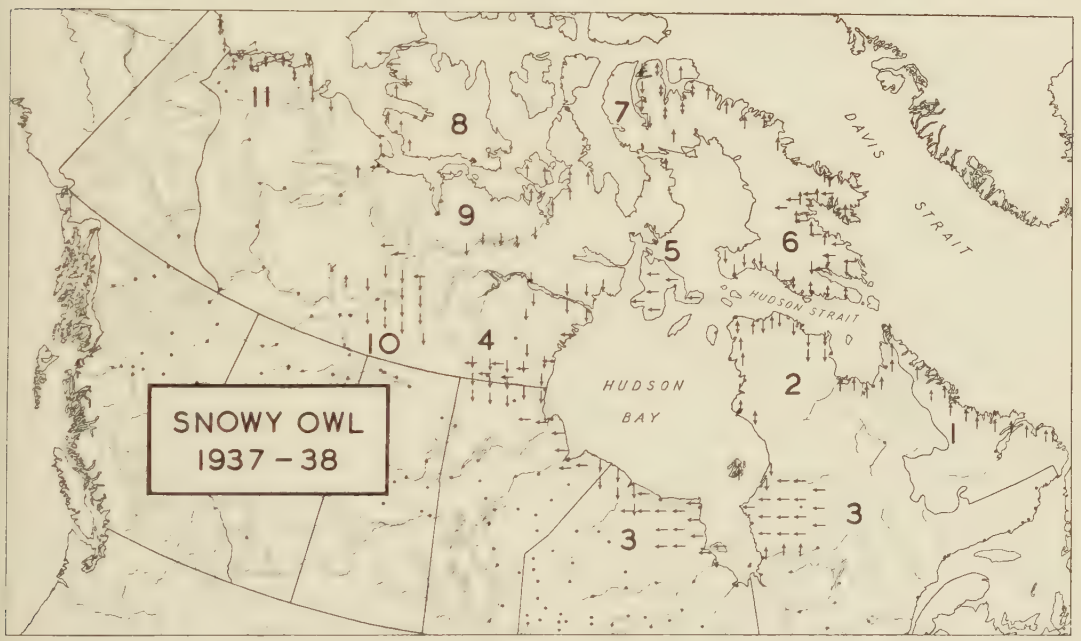

Fig. 4.

Figs. 3, 4. State of the lemming and snowy owl populations in 1937–38 compared with 1936–37. Arrows indicate areas covered by observers reporting Increase (↑), Decrease (↓), and No change, not abundant (←), No change abundant (→). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

Baillie Island to the Mackenzie delta. In places the start of this upward swing had been observed in 1936–37. Inland from Back River and Bathurst Inlet no significant trend in the lemming population has become apparent during 1935–38.

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1937–38. *Number of observers reporting relative abundance compared with* 1936–37

	Eastern Arctic								
Group no. ...	1	2	3	4	5	6	7	Total	%
Arctic fox:									
Increase	11	9	9	7½	2	6	5	49½	**82**
Decrease	1	3	1	2	—	—	—	7	**12**
No change	—	—	1	2½	—	—	—	3½	**6**
	12	12	11	12	2	6	5	60	**100**
Lemming:									
Increase	6	12	—	1	2	6	1	28	**67**
Decrease	—	1	—	7	—	—	1	9	**21**
No change	—	—	—	3	—	—	2	5	**12**
	6	13	—	11	2	6	4	42	**100**
Snowy owl:									
Increase	10	7	2	—	—	2	2	23	**42**
Decrease	—	5	2	6	—	3	2	18	**33**
No change	1	—	6	5	1	1	—	14	**25**
	11	12	10	11	1	6	4	55	**100**

	Western Arctic					
Group no. ...	8	9	10	11	Total	%
Arctic fox:						
Increase	5	—	3	4	12	**50**
Decrease	1	—	1	4	6	**25**
No change	—	1	3	2	6	**25**
	6	1	7	10	24	**100**
Lemming:						
Increase	5	—	3	5	13	**54**
Decrease	—	—	1	2	3	**13**
No change	1	1	3	3	8	**33**
	6	1	7	10	24	**100**
Snowy owl:						
Increase	2	—	1	4	7	**39**
Decrease	1	—	2	3	6	**33**
No change	1	—	3	1	5	**28**
	4	—	6	8	18	**100**

Arctic fox. From Cartwright to Port Burwell and west to Fort Chimo all observers reported an increase in arctic foxes. This was a decided improvement on the two years 1935–36 and 1936–37, when respectively 1 out of 12 and 4 out of 13 reports of increase were received. In 1936–37 increase was reported all the way from Leaf River to Port Harrison. This trend was only partly maintained in 1937–38, as from Leaf River to Stupart Bay decrease or great scarcity was reported. A decided improvement is shown by the figures for increase in group 3, which in three years have risen as follows: 0 out of 10, 3 out of 9, 9 out of 11. The increase in groups 1 and 3 (largely outside the breeding range) is probably because of southward movements: the result of increased populations further north. The majority of reports were of increase

over the following huge circuit: from Churchill up the west coast of Hudson Bay and inland; north-east to the tip of Melville Peninsula; the islands of Southampton, Baffin, Ellesmere, Somerset, Victoria and King William; south of Dease Strait, in Adelaide and Boothia Peninsulas, Back River, to Baker Lake. Of the 31 observers in these regions only six reported decrease or no change among arctic foxes. Five of these covered a belt north and south of the boundary between Manitoba and the Northwest Territories (from Eskimo Point, no change was reported to the south and increase to the north-west) and the other was in the north-west of Victoria Island. In groups 5, 6 and 7 this was the second year in which little but increase was recorded; but in groups 8 and 9 and at Chesterfield Inlet and Baker Lake (group 4) these were almost the first signs of recovery.

The increase apparent as far west as the east part of group 9 does not seem to have occurred at Bathurst Inlet or inland to the south and west. Along the coast west of the Coppermine River and east of Richards Island there seems to have been some improvement on the previous year although there is some conflicting evidence about this.

Snowy owl. Two changes in the trend of snowy owl populations are indicated: (1) increase throughout group 1 and west to Leaf River; (2) partial decrease in Baffin Island where nothing but increase was observed in 1936–37. Elsewhere, except that there were fewer reports of increase in groups 3 and 4, it is hard to get any clear picture of what was happening. It can only be noted that in groups 8 and 11 half the 12 observers stated that increase had occurred; compared with one-third the previous year.

In certain winters abnormally large numbers of snowy owls are observed far south of their normal range, and it is believed that these southern flights are connected with the failure of the owls' food supply in the north. In view of the importance of testing this belief by correlating the southern flights with the date of the present enquiry, Mr Charles Elton suggested that a special enquiry should be made in the southern parts of Canada. This seemed particularly desirable since some other reports received indicated that snowy owls had appeared in some places in south-eastern Canada in greater numbers than usual during the early winter of 1938–39. The National Parks Bureau arranged to send out a questionnaire and obtained some useful facts. It is not proposed, however, to discuss them here because they can best be treated in connexion with the next year's report, and because the whole matter of the southern flights of the snowy owl is now being studied by a group of Canadian and American biologists who will be able to conduct a wider and more thorough survey, and with whom the Bureau of Animal Population will co-operate closely.

Sledge dog. The general situation is fairly clear from Table 3 and Fig. 2: an epidemic down the lower Mackenzie River valley, a few outbreaks of disease widely scattered across the continent, and otherwise nothing serious.

Table 3. *Information about sledge dogs*, 1937–38

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

(*a*) *Disease or epidemic reported.* (More serious outbreaks indicated +.)

Quebec and Labrador.

\+ *Natashquan.* "Quite a few dogs died in the early part of the winter. Sickness same as in previous outfit—unknown."

\+ *Senneterre.* "Disease prevalent amongst sledge dogs during summer and fall months. Symptoms: swelling of joints and running matter from the nose."

\+ *La Sarre.* "Sledge dogs kept from 50 to 100 miles north of here were affected by disease during July and August 1937, many died. Symptoms were swelling of the throat and the joints of the legs, with running matter from the nose. These symptoms usually developed about three weeks before death. Sledge dogs kept about 30 miles north of the post developed and died of this disease during the period Sept.–Dec. 1937." (2+)

Port Burwell. "Disease in Feb. and Mar. Only symptoms were lack of energy and no desire to eat."

\+ *Great Whale River.* "Sickness practically all winter. Quite a number have died."

Ontario.

\+ *Ombabika.* "Nearly all the Indian dogs had some kind of disease, got thin and died last summer."

\+ *Fort Hope.* "An epidemic occurred among sledge dogs last fall killing most of them."

Bearskin Lake. "Sledge dogs were subject to epidemic last winter (local, not general). During the coldest weather a few of the dogs got sick: went off their feed, coats got very shaggy. No other symptoms."

Manitoba.

\+ *Island Lake.* "Several sledge dogs took sick during the winter and all efforts failed to fatten them up. Several died during the break-up period in a very bloated condition."

\+ *Shamattawa.* "Distemper spread amongst the sledge dogs at the beginning of the warm weather in May 1937. Lasted all summer until fall 1937. 50% died."

\+ *York Factory.* "June–Aug. several sledge dogs died with a disease having the following symptoms: running discharge from eyes and nose, sneezing and staggering."

Saskatchewan.

\+ *Clear Lake.* "Dysenteric epidemic among dogs in August 1937. 60% animals affected with 50% mortality."

Fond du Lac. "Mild epidemic of distemper during the winter, but fully recovered in the early spring. Very few deaths reported."

10. *Lake Athabasca.* "Distemper quite common...striking at intervals."

British Columbia.

\+ *Nelson Forks.* "There appeared to be a disease among sledge dogs this winter and several had to be destroyed. The animals first would not eat, grew thin and weak, and what appeared to be a kind of paralysis set in."

Northwest Territories.

1. Baffin Island

32. *Lake Harbour.* "Two pups died."

Clyde River. "Sickness in middle of winter. Vomiting gall: perhaps undernourished."

2. Great Slave Lake Region

\+ *Rocher River.* "Distemper in Jan. and Feb. Quite a number died."

Fort Reliance. "Excess salivation, running eyes, 'hysteria', paralysis (in order given) was going on in the R.C.M.P. teams at Reliance 18–19 June, 1937. No deaths up till then." (Report No. 31 of 1936–37 enquiry.)

5. *Fort Reliance.* "Running about, yelping and frothing at the mouth, in June."

\+ *Fort Providence.* "Six dogs died this spring of distemper, mostly pups. All dogs in bush reported O.K."

Table 3 (*continued*)

\+ **11.** *Fort Providence.* "Distemper was first noticed in the Tathlina Lake area in latter March and eventually broke out in this settlement."

Hay River. "No noticeable disease among dogs but about 3 or 4% suffered from paralysis in lower back and hind quarters during Nov. and Dec. About 20% of these died: all old dogs."

3. Mackenzie River Valley

Fort Norman. "Several isolated cases of distemper. The disease appeared to come from Fort Good Hope to Burnt Lake and from there into Fort Norman. In March two pups and one dog died. Dogs became paralysed in hind quarters."

\+ **3.** "*Forts Norman* and *Good Hope* (Jan., Feb.) and *McPherson* (Apr.) had many fatal cases of distemper. Milder at *Aklavik* where a few cases occurred towards the end of May." (4+)

\+ *Fort Good Hope.* "A lot of dogs died with distemper in the Fort and in the Indians' camps in the bush. Some Indians said that their dogs had died of some other, unknown, sickness."

\+ **26.** *Fort Good Hope.* "Animals first appeared very listless, some dry-eyed, others with heavy yellow mucus continually running from eyes. From one day to a week later dogs became partly paralysed in legs on one side of body, running into objects as if unable to see. They were taken with cramps, vomited, or tried to, became considerably weakened and died. First noticed here in the last week in Feb., continuing among most dogs, some of which recovered. Numbers lost: R.C. Mission, three out of six; R.C.M.P., five out of eight; Indians, nine out of about 30. The middle of March it was reported among the dogs at the headwaters of Ramparts River where some 60 dogs died out of 180. The end of March a few cases were reported at Coville Lake and Lac des Bois. There are about 100 dogs in that district and about six died out of twelve affected." (3+)

\+ **24.** *Fort Good Hope.* "Distemper. Nov.–Feb. Dogs refuse food and die in a week."

\+ *Arctic Red River.* "Quite a lot of dogs died from distemper during winter and spring."

\+ *Fort McPherson.* "A severe epidemic of distemper occurred among sledge dogs in this region immediately after Indians had made a trip to Fort Dawson in the Yukon. Many dogs succumbed quickly."

\+ *Aklavik.* "Disease prevalent during spring months. Symptoms: running at nostrils and eyes, refuse food. No signs of madness. White trappers and natives both losing dogs."

\+ **17.** *Aklavik to coast.* "Discharge of matter from eyes and nose. Paralysis of hind-quarters, obvious congestion of lungs and in some cases blindness. Occurred in late April and May. The epidemic was evidently distemper and from reports travelled down the river from Fort Good Hope, attacking dogs at Arctic Red River and Fort McPherson, being carried from post to post by visiting dog teams. This disease was not the so-called 'crazy disease': none of the dogs ran about or foamed at the mouth. The R.C.M.P. at Aklavik lost 13 dogs. The disease appeared to take greater toll of the younger dogs, although some of the old dogs died from it. Other dogs died in the settlement, but some groups took only a very mild form of it and recovered."

\+ **14.** *Mackenzie River Delta.* "Dogs lost appetite and died sometimes within a week; in some cases with a froth round the eyes and mouth. Some recovered. Started about Christmas and still continues (15 June). May have been some form of distemper, probably brought by Indians from Dawson."

(*b*) *Disease reported absent* (see also Table 1)

Quebec. Seven Islands. Bersimis. Weymontachingue. Oskelaneo. Woswonby. Chibougamau. Mistassinny. **Ontario.** Missanabie. Mattice. Grassy Narrows ("*very few dogs*"). Moose Factory. Windigo. Deer Lake. Trout Lake. **Manitoba.** Rossville. Norway House. God's Lake. Cross Lake. Wabowden. Gisipigimack. Pukatawagan. Granville Lake. South Indian Lake. **Saskatchewan.** Pelican Narrows. Lac la Ronge. Stanley. Souris River. Pine River. Buffalo River. South Reindeer Lake. **Alberta.** Fort McKay. Fort Chipewyan. Hay Lakes. Upper Hay River. Fort Fitzgerald. **British Columbia.** Fort St James. Tacla. Fort Nelson. **N.W. Territories. 27.** Southampton Island. Fort Smith. Fort Liard (also **7**). **13.** Fort Providence. [**4.** Flat River, McMillan Lake and Bennett Creek locality via Fort Simpson.] **2.** Arctic Red River to Aklavik and Fort Good Hope ("*No epidemic of disease for* 15 *years*"). **9.** Point Separation.

There is some disagreement among the reports about dates, about whether or not disease was present at all, and if so how serious it was. Few reports are as good as no. 26 from Fort Good Hope, which gives symptoms, dates and the number of dogs affected out of the total at risk. Without a greater amount of similarly detailed information the + symbols on the map must necessarily be of rather arbitrary significance. However, the records have shown the absence, during the three years 1935–38, of any pandemic among sledge dog teams.

The symptoms indicate that it was mainly so-called "distemper" and not "crazy disease" present in the afflicted regions. Information in the reports about diet and its possible relation to the outbreaks is being kept on file.

4. Summary

1. 105 answers were received to questionnaires on population trends during 1937–38 of lemmings (*Lemmus* and *Dicrostonyx*), arctic foxes (*Alopex lagopus*) and snowy owls (*Nyctea nyctea*) in the Canadian Arctic.

2. Lemmings, "mice", arctic foxes and snowy owls were reported on the increase up most of the Labrador coast and west to Fort Chimo.

3. At the four posts Leaf River, Payne Bay, Diana Bay and Stupart Bay foxes were scarce, at three of them snowy owls had decreased, but only at Diana Bay was there a correlation with decrease in lemmings.

4. Lemmings increased further west in Hudson Strait and south to Port Harrison. In the same area, and also south to Eastmain, there was marked increase in foxes; but not to the same extent in snowy owls.

5. There was an improvement in foxes from Baffin Island (second year of recovery) to the west coast of Victoria Island (first year of recovery) and south-east over 1000 miles to the south shore of Hudson Bay (but excluding parts of the west shore). This increase corresponded with reports of increase or abundance among lemmings in southern Baffin Island and parts both of northern Baffin Island and of Victoria Island. Elsewhere, the correlation was less general. Snowy owls showed signs of decreasing on Baffin Island, perhaps foreshadowing a decrease in lemmings, for which there was evidence in the reports.

6. West and south from Bathurst Inlet conditions had improved very little; but between the Coppermine River and the Mackenzie delta increase in all three species was more commonly reported than in the previous two years 1935–37.

7. Sledge dogs were on the whole free from epidemics but a severe outbreak of "distemper" occurred throughout the lower Mackenzie River Valley.

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POPULATIONS OF *THRIPS TABACI*, WITH SPECIAL REFERENCE TO VIRUS TRANSMISSION[1]

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(*With Plate* 10 *and* 4 *Figures in the Text*)

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1. Introduction

Thrips tabaci Lind., the onion thrips, is an insect of world-wide distribution, and with an extensive host range. Within recent years it has been shown to be the vector of virus diseases (2, 4, 5) of the type that require an incubation period in the insect vector, and in which, virus, vector, and host plant comprise an inseparable ecological trinity. It was with the object of determining the seasonal fluctuation of *T. tabaci* populations, and the relationships between these and disease incidence that this study was initiated.

2. Methods

Apart from onions, one of the most widely distributed and favoured host plants is *Emilia sonchifolia* DC. This species was referred to by Linford (2) as *Emilia sagittata* (Vahl) DC. St John & Hosaka have later (3) established *Emilia sonchifolia* DC. as the correct name. It is one of the first weeds to appear following denudation from cultivation, clearing, road grading or the like. It was early shown (2) to be an important host for yellow spot virus. This host was therefore chosen as most satisfactory for the purpose of this study. Samples were taken from four places chosen primarily to represent different conditions of rainfall and to a lesser degree, temperature.

The usual method was to collect the *Emilia* plants by traversing the area

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[2] The collection of data on which this paper is based has been a departmental activity. Special acknowledgements are due to Mr K. Ito who collected the samples, and Mr K. Sakimura who prepared the data from wind traps. Determination of thrips species were made by Mr Sakimura and D. Moulton.

and pulling one plant every five paces. These plants were bagged together for each area and on the following day were separated, the thrips removed by shaking onto a black cloth, the leaves carefully examined and the flowers, if any, dissected. This method involved some possibility of movement by thrips among the plants while the latter were conglomerated, but since total populations were used to obtain average populations per plant sampled, such movement, if any, would not affect the data presented. Evidence that such movement does not occur significantly, however, is available in the data of which Table 5 is the summary. Although diseased and healthy plants were mixed indiscriminately in the sample bags, the average populations on the diseased plants were higher than on the healthy plants. Averages only are shown in Table 5 but the individual data show a high degree of consistency.

The stage of growth of the host plant presented some difficulty. In view of its rapid growth, free flowering, senescence and frequent re-seeding, plants of all sizes and conditions of growth were included in a single sample. To include some measure of these differences, plants were measured as to length, and the number of flower-heads, if any, recorded. Since no relationship between detailed plant measurements and *Thrips tabaci* populations is apparent from the data, these details have been omitted from the tabulation.

With the intrusion of other plants, particularly grasses, the *Emilia* stage of succession would pass from the original location, in which case some immediately contiguous area was chosen. In the type of cultivation in practice, pineapple fields are found in any one locality in all stages from fallow, through freshly planted fields, to old fields in which cultivation has ceased. There is therefore, a situation which permits *Emilia* to flourish essentially without interruption. While the plants were being examined for thrips they were also inspected for symptoms of yellow spot and diseased plants recorded.

Data on flight of *Thrips tabaci* were obtained by means of tanglefoot screens fastened to a frame which was kept headed into the wind by means of a large rudder. Tanglefoot screens were substituted for wire screens as described by Fulton & Chamberlin(1), owing to the difficulty of recovering thrips from the collection jars used by those workers.

3. *Thrips tabaci* populations and disease in *Emilia*

Data from all four stations are presented in Tables 1–4 and in graphic form in Figs. 1–4. An aerial photograph of one station (Area 3, Kipapa) is shown on Plate 10.

Although population density varies widely between locations, the seasonal trend is similar at all four points, with populations decidedly lower in the winter months. This is true of populations per plant as well as percentage of plants infested and from these data it may be deduced that the total populations in the several areas fluctuated similarly. The lag between the curves

Table 1. *Area* 1, *Kunia, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
5 Apr.	177	13·56	0·19	11·86	
1 June	135	27·40	0·9	1·48	
3 July	227	29·95	0·67	1·32	Practically no diseased *Emilia*. Succulent young growth abundant
3 Aug.	140	17·85	0·37	2·85	
7 Sept.	160	6·87	0·10	11·87	Field becoming weedy along periphery. Luxuriant new growth of *Emilia*. Few diseased
2 Oct.	114	2·63	0·02	3·50	Luxuriant growth of *Emilia*
1 Nov.	100	12·00	0·19	1·00	*Emilia* within field area old. Field recently weeded
18 Dec.	134	10·45	0·20	2·99	Fair growth, very few diseased
1935:					
8 Jan.	129	3·88	0·05	1·55	Growth good in field area. Very few diseased plants
7 Feb.	142	2·81	0·04	1·41	Luxuriant *Emilia*, very few diseased
6 Mar.	146	6·16	0·13	9·58	Good growth of *Emilia*. (These records were taken approximately 1 week after heavy rains and floods)
4 Apr.	120	5·00	0·08	1·66	Field weedy
7 May	56	26·79	0·84	0	Field generally weeded. Very few *Emilia*. Picked all available
7 May	111	36·94	0·82	18·02	*Emilia* fairly common
13 June	99	7·07	0·13	2·02	Very few *Emilia* along periphery. Too dry. Sampling transferred to contiguous field
9 July	82	2·43	0·02	3·66	Few *Emilia*, very dry
14 Aug.	82	0	0	1·22	Very few scattered *Emilia* plants between beds. Picked all available. Practically no *Emilia* along periphery, too dry. Other weeds dried also
12 Sept.	55	0	0	5·45	Picked all available *Emilia* at not less than 5 pace intervals. Very few weeds along periphery. Horseweeds reviving after recent showers
11 Oct.	145	0·68	0·01	2·06	Fair growth of new *Emilia* seedlings
14 Nov.	228	2·63	0·03	0·88	
13 Dec.	141	9·93	0·14	0·71	Area ploughed; contiguous field sampled. *Emilia* luxuriant and fairly abundant, very few diseased
13 Dec.	235	0·43	0·004	0	*Emilia* abundant along periphery, mostly new seedlings, none diseased. Area ploughed

Table 2. *Area* 2, *Wahiawa, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
5 Apr.	95	9·47	0·42	0	*Emilia* abundant but growth coarse
1 June	75	25·33	0·42	0	
3 July	147	39·45	1·57	10·20	Spring growth of *Emilia*
3 Aug.	184	11·41	0·16	6·52	
7 Sept.	110	0·90	0·009	5·45	Recently weeded; few *Emilia* except along periphery. New growth on old stock
2 Oct.	125	6·40	0·07	8·80	New growth of *Emilia*
1 Nov.	158	13·92	0·21	0·63	
18 Dec.	124	16·13	0·25	6·45	Fair growth of *Emilia*: few diseased
1935:					
8 Jan.	146	6·16	0·10	4·79	
7 Feb.	111	10·81	0·22	1·80	Recently weeded; few *Emilia*
6 Mar.	126	19·05	0·28	6·35	Fair growth of *Emilia*: few diseased. (Notes taken about one week after heavy rains and floods)
4 Apr.	107	36·45	0·95	11·22	*Emilia* not so abundant but common enough for adequate sample
7 May	108	76·85	6·11	25·00	*Emilia* mostly healthy and young
13 June	145	38·62	1·00	17·93	Few *Emilia*; dry and recently weeded
9 July	64	15·62	0·20	37·50	Dry and recently hoed. Very few *Emilia*—picked all available
14 Aug.	105	15·24	0·38	17·14	Picked all available *Emilia*
12 Sept.	92	6·52	0·16	6·52	Very few *Emilia*; few weeds in field
11 Oct.	109	38·53	1·05	2·75	
14 Nov.	89	10·11	0·16	6·74	
13 Dec.	140	11·43	0·16	5·00	*Emilia* abundant, luxuriant growth. Mainly new seedlings with very few diseased plants

Table 3. *Area* 3, *Kipapa, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
7 Mar.	104	56·73	1·50	28·85	Plate 10, 2 A. *Emilia* growth luxuriant. Fair number of diseased plants
5 Apr.	128	57·81	2·28	14·84	
1 June	112	72·32	3·48	32·14	
3 July	152	67·10	2·94	50·00	Diseased *Emilia* prevalent
3 Aug.	110	50·90	2·00	46·36	
7 Sept.	128	10·93	0·18	33·54	Very little new growth; plants mostly old and diseased; field weedy
2 Oct.	122	19·67	0·41	57·37	Field weedy
1 Nov.	158	5·63	0·06	6·96	Field weedy. New growth of *Emilia* shows few diseased plants
18 Dec.	131	0·76	0·01	6·87	Luxuriant new growth. Few diseased plants
1935:					
8 Jan.	117	0	0	6·84	Luxuriant new growth. Very few diseased plants
7 Feb.	133	0	0	0·75	Luxuriant *Emilia*. Field becoming very weedy
6 Mar.	152	1·32	0·01	0	Field weedy but *Emilia* plentiful and mostly healthy. (These records were taken approximately one week after heavy rains and floods)
4 Apr.	134	6·72	0·09	0	Field very weedy
7 May	57	5·26	0·07	1·75	Dry: only few old *Emilia*
13 June	137	46·72	1·34	38·69	Plate 10, 2 B. *Emilia* abundant; majority diseased, dry
9 July	190	14·73	0·24	57·89	Dry, but fair number of *Emilia* plants
14 Aug.	221	29·41	0·63	57·47	*Emilia*, mostly old stand, fairly common but rather withered. Natal and crab grasses predominant. Dry
12 Sept.	169	11·24	0·22	53·25	No new *Emilia* seedlings, all new growth on old stocks
11 Oct.	179	36·87	1·11	43·57	Area becoming too weedy with grass for healthy *Emilia* growth. *Emilia* mostly of old stock, some new seedlings
14 Nov.	118	5·08	0·09	27·11	Area ploughed up after sampling
13 Dec.	110	2·73	0·04	13·64	Plate 10, 2 C. *Emilia* seedlings still small; picked all available

Table 4. *Area* 4, *Waimea, Oahu. Populations of* Thrips tabaci *and incidence of yellow spot disease in* Emilia sonchifolia

Date	No. of plants sampled	% plants thrips infested	Av. no. of thrips on plants sampled	% plants diseased	Notes
1934:					
1 June	125	51·20	1·35	53·60	
3 July	157	46·49	1·12	29·93	Field was weeded just prior to sampling date
3 Aug.	165	70·30	5·31	78·18	
7 Sept.	147	58·50	2·08	63·94	Nearly all old diseased *Emilia*. New growth scanty
2 Oct.	136	45·58	1·28	30·88	Field weeded. Very little *Emilia*. Peripheral vegetation wilting due to drought
1 Nov.	144	16·66	0·26	40·27	Very little new growth due to recent weeding
18 Dec.	164	17·07	0·27	16·46	Fair growth of *Emilia* along uncultivated edges. Field proper recently cultivated
1935:					
8 Jan.	170	27·65	0·68	42·94	Little new growth, majority of the older plants diseased
7 Feb.	139	67·62	2·97	46·04	Good growth of *Emilia*, fair amount of disease in old specimens
6 Mar.	204	44·11	1·06	24·02	Field recently weeded; few *Emilia*. (These records were taken approximately one week after heavy rains and floods)
4 Apr.	151	53·64	1·82	26·49	Few *Emilia*; field recently weeded
7 May	157	49·68	1·62	25·48	Few *Emilia*; field recently weeded
13 June	210	48·09	1·27	48·09	Field weedy with young weeds. *Emilia* fairly common, good growth, mostly diseased
9 July	166	38·55	0·74	60·84	Good growth of *Emilia*; some disease among young seedlings
14 Aug.	139	40·29	1·28	38·13	*Emilia* fairly common and in fair state of growth. Field weedy mainly with crab grass
12 Sept.	165	14·54	0·30	23·63	Crab grass predominant with horseweed interspersed. Fair *Emilia* growth, few diseased
11 Oct.	153	42·48	1·22	20·91	Field very weedy; *Emilia* fairly common in field
14 Nov.	170	35·88	1·10	37·05	
13 Dec.	154	30·52	0·51	29·22	Field very weedy with grasses and horseweed. *Emilia* luxuriant along periphery and field road as well as in the field. Mostly new growth with a fair number diseased

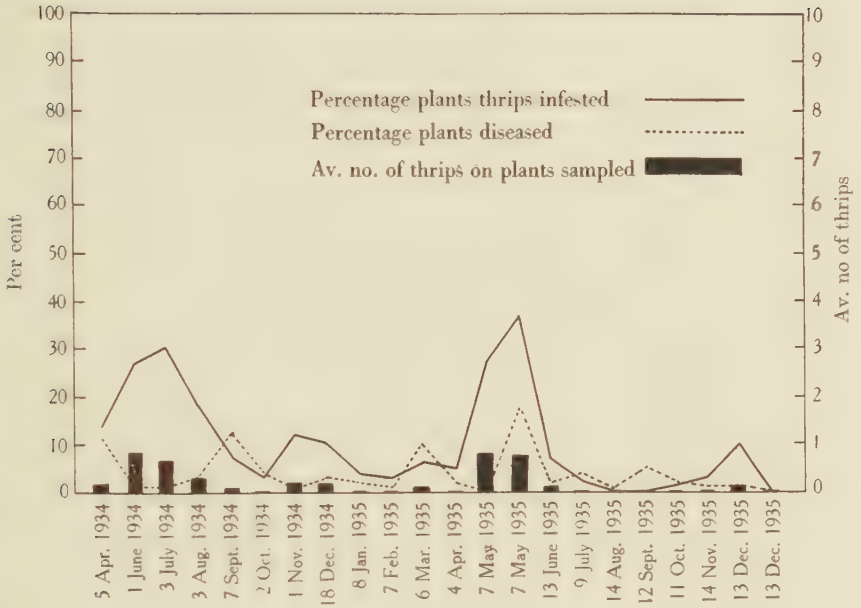

Fig. 1. Data from Area 1, Kunia, Oahu.

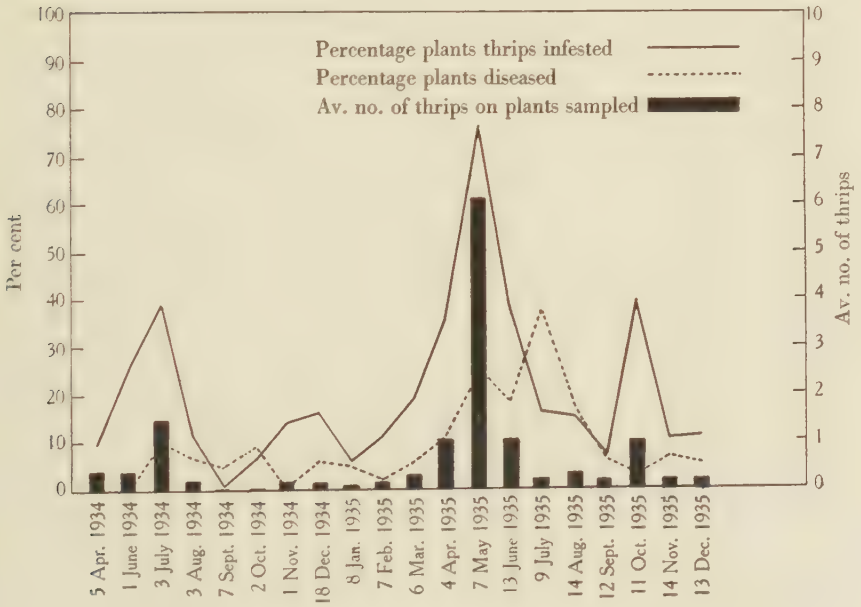

Fig. 2. Data from Area 2, Wahiawa, Oahu.

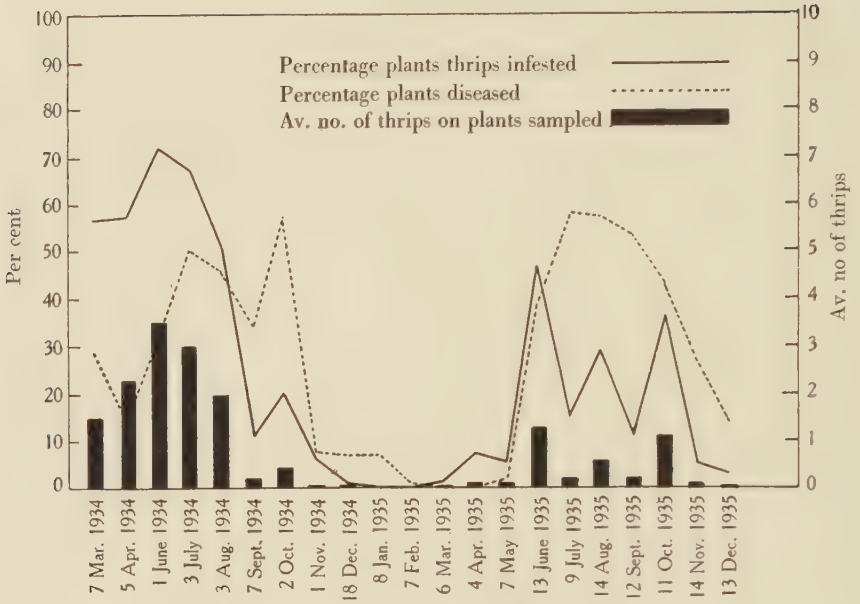

Fig. 3. Data from Area 3, Kipapa, Oahu.

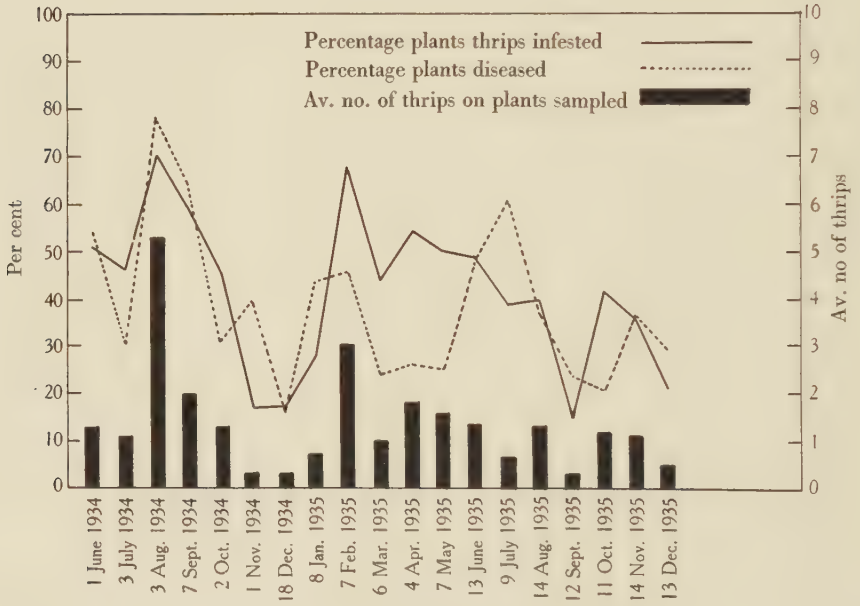

Fig. 4. Data from Area 4, Waimea, Oahu.

showing percentage of plants infested and percentage diseased is understandable when the incubation period of the disease in the plant is considered. The similarity of the two curves, however, strongly suggests that the thrips colony is sedentary and once established on an *Emilia* plant there is little movement even to other *Emilia* in the near vicinity. Any tendency on the part of *Thrips tabaci* to pass freely to and fro among *Emilia* plants would be strongly reflected in the percentage of plants diseased since only a short period of feeding by *Thrips tabaci* is necessary to infect the plant.

The only exception is seen in Fig. 3 where the divergence between the percentage of plants infested and the percentage of plants diseased in July, August and September, 1935, indicated either sudden reduction of thrips infestation by some environmental factor or the movement of viruliferous thrips from *Emilia* to *Emilia*.

Comparison of Thrips tabaci *populations on diseased and healthy* Emilia

When the plants collected from each locality are separated into the two categories of healthy and diseased and the thrips populations on the two considered, it is seen that the populations on diseased *Emilia* are consistently higher than those on healthy *Emilia*. All the data in this connexion are summarized in Table 5.

Table 5. *Summary of data from four collection areas showing relative thrips populations on diseased and healthy* Emilia sonchifolia

Collection locations, Oahu	No. of healthy plants infested	No. of *Thrips tabaci* on infested healthy plants	Average population on infested healthy plants	No. of diseased plants infested	No. of *Thrips tabaci* on infested diseased plants	Average population on infested diseased plants
Area 1, Kunia	278	598	2·2	28	55	2·0
Area 2, Wahiawa	406	1124	2·8	92	518	5·6
Area 3, Kipapa	358	1024	2·9	329	1204	3·7
Area 4, Waimea	628	1520	2·4	666	2697	4·0

The explanation for this is probably that while healthy *Emilia* normally grows rapidly, matures and dies, diseased plants may persist for a longer time with a mass of curled leaves affording satisfactory shelter for *Thrips tabaci*. It seems to be demonstrated that when *Emilia* functions as a reservoir of the yellow spot virus it is also a more suitable host for *Thrips tabaci*.

Although the collection of data from relatively restricted localities is a valid method of obtaining seasonal trends of insect populations, it cannot be presumed that such populations are homogeneous over a large area even under Hawaiian conditions, where seasonal changes are slight and violent disruption of host plant sequence rarely occurs.

Occasionally additional collections were made at points fairly contiguous to the regular collecting places and the data from these are listed in Table 6 where comparisons are possible between them and the regular collections.

It is evident that population densities are not homogeneous and "pockets" may occur wherein deviation from a standard collection point can be found.

Table 6. *Comparing data from regular collecting points with data obtained at nearby locations on same dates*

Location	No. of plants sampled	% infested	Average *Thrips tabaci* population	% diseased	Notes
Date: 7 March 1934					
Kipapa, Area 3, 2 A, Plate 10	104	56·73	1·50	28·85	Regular collecting point. *Emilia* growth luxuriant; diseased plants in fair number
Kipapa 2 D, Plate 10	66	6·06	0·08	0	Fallow field in grass: *Emilia* abundant and luxuriant
Date: 5 April 1934					
Kipapa, Area 3, 2 A, Plate 10	128	57·81	2·28	14·84	Regular collecting point. *Emilia* luxuriant: fair number of diseased plants
Kipapa 2 E, Plate 10	61	54·10	1·30	22·95	Along drainage ditch
Date: 7 May 1935					
Kipapa, Area 3, 2 A, Plate 10	57	5·26	0·07	1·75	Regular collecting point. Dry: only few old *Emilia* plants
Kipapa 2 F, Plate 10	275	90·91	10·93	60·73	No record
Date: 5 April 1934					
Wahiawa	95	9·47	0·42	0	Regular collecting point. *Emilia* abundant: growth coarse
Wahiawa A	20	30	0·3	6·7	Area recently weeded: *Emilia* scarce
Wahiawa B	54	11	0·11	0	*Emilia* abundant

4. Records of flight obtained from trap catches

Three tanglefoot traps were maintained in the area covered by systematic collections at Kipapa, Area 3 (Plate 10, 1 A, B, C). After 2 months two of the traps were removed from the original positions to the periphery of a nearby field in which detailed counts on the incidence of yellow spot in pineapples were to be taken (Plate 10, 1 D, E). Although this paper is concerned primarily with *Thrips tabaci*, all the thrips collected are listed in Tables 7 and 8, because no data on wind-borne thrips species have been published, and the comparative catches of *Thrips tabaci* and other species are significant.

It will be noted that *Thrips tabaci* occupies an extremely minor position both with respect to incidence and numbers caught. On the other hand *Taeniothrips hawaiiensis* is found almost without exception in all the collections with high populations in the winter months. *Stulothrips trespinus* shows an interesting distribution. At both places it appeared in the late August collection in small numbers. From October on to the end of the year, its incidence and numbers are both high. The large numbers at trap locations 1 D and E in October indicate a mass movement of considerable proportions. At both trap locations, the incidence of this species was high for the rest of the year.

It is interesting to note that most of the species listed attain their greatest incidence and numbers during the late fall and winter months. Several of

(Photo by Eleventh Photo Section, A.C., Wheeler Field, T.H. Published by permission).

Phot. 1. Aerial photograph of Area 3, Kipapa, Oahu:

1A to E—Wind traps.
2A to F—*Emilia* samples.
3A to H—Yellow spot samples.
4A to C—Yellow spot samples.

Table 7. *Area* 3 (*Plate* 10, 1 A, B, C). *Thrips caught in wind traps*

		Terebrantia, Thripidae											Tubulifera, Phloeothripidae									
Date	Trap	*Heliothrips rubrocinctus* (Giard)	*Chirothrips mexicanus* Crawford	*Taeniothrips hawaiiensis* (Morgan)	*Thrips abdominalis* Crawford	*Thrips panicus* Moulton	*Thrips saccharoni* Moulton	*Thrips tabaci* Lind.	*Isoneurothrips carteri* Moulton	*Isoneurothrips fullawayi* Moulton	*Stulothrips trespinus* Moulton	*Hoplothrips flavitibia* Moulton	*Hoplothrips paumalui* Moulton	*Aleurodothrips fasciapennis* (Frank.)	*Haplothrips fusca* Moulton	*Haplothrips gowdeyi* (Frank.)	*Haplothrips melaleuca* Bagnall	*Haplothrips* (*Hindsiana*) *sakimurai* Moulton	*Haplothrips williamsi* Moulton	*Kentronothrips hawaiiensis* Moulton	Undetermined
1935:																						
20 May	1 B	.	.	1	.	.	.	4	.	.	.	.	.	1	.	2	.	.	.	.	.
22 May	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25 May	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8 June	1 A	.	.	4	.	.	.	.	.	1	.	.	.	1	.	1	1	.	.	.	.
	1 B	.	.	4	1	.	1	1	1	.	.	.	.	.	.	2	.	.	1	.	.
	1 C	.	.	4	1	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.
13 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	1 B	.	.	4	.	.	1	.	.	.	.	.	.	.	.	1	1	.	.	1	.
	1 C	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1	.
19 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	1	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2
	1 C	.	.	4	.	1	.	.	.	1	.	.	.	.	.	2	1	.	.	.	.
28 June	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.
	1 B	.	.	7	1	.	.	.	.	1	.	.	.	.	.	2	2	1	.	.	.
	1 C	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5 July	1 A	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	2	2	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.
10 July	1 A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
	1 B	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18 July	1 A	.	.	3	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
	1 C	.	1	2	.	.	1	.	.	.	.	.	.	.	.	3	1	.	.	1	.
24 July	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.
31 July	1 C	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
8 Aug.	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
14 Aug.	1 C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
22 Aug.	1 C	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.
31 Aug.	1 C	.	.	2	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.
6 Sept.	1 C	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.
12 Sept.	1 C	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.
18 Sept.	1 C	.	.	4	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.	.	1
27 Sept.	1 C	.	.	3	.	1	8	.	.	.	.	.	.	.	.	1	.	.	.	6	.
4 Oct.	1 C	.	.	.	.	.	2	.	.	.	.	.	.	.	.	1	.	.	.	2	.
11 Oct.	1 C	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.
18 Oct.	1 C	.	.	5	1	.	3	.	.	.	5	.	.	.	.	.	.	2	.	.	.
25 Oct.	1 C	.	.	4	.	.	2	.	.	.	2	.	1	.	.	2	.	1	.	.	1
1 Nov.	1 C	.	.	8	.	.	.	.	.	.	.	.	1	.	1	2	.	2	.	.	.
8 Nov.	1 C	.	.	11	1	.	.	.	.	.	15	.	.	.	.	.	.	2	.	.	.
22 Nov.	1 C	.	2	19	1	.	1	.	.	.	4	.	.	.	.	.	.	1	.	1	.
29 Nov.	1 C	.	.	8	.	.	.	.	.	.	17	.	.	.	.	2	.	.	.	2	.
6 Dec.	1 C	.	.	.	2	.	.	.	.	.	4	.	.	.	.	1	.	.	.	2	.
13 Dec.	1 C	1	.	3	.	.	.	.	.	.	3	.	.	.	.	3	.	.	.	4	.
20 Dec.	1 C	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.
30 Dec.	1 C	3	1	14	3	.	3	2	.	.	2	.	.	.	.	6	.	2	.	1	.
1936:																					
3 Jan.	1 C	.	2	1	.	1	.	.	.	.	2	.	.	.	.	1	.	.	.	.	.

Table 8. *Area* 3 (*Plate* 10, 1 D, E). *Thrips caught in wind traps*

Date	Trap	*Heliothrips haemorrhoidalis* Bouché	*Heliothrips rubrocinctus* (Giard)	*Chirothrips fulvus* Moulton	*Chirothrips mexicanus* Crawford	*Chirothrips sacchari* Moulton	*Taeniothrips hawaiiensis* (Morgan)	*Thrips abdominalis* Crawford	*Thrips paniceus* Moulton	*Thrips saccharoni* Moulton	*Thrips tabaci* Lind.	*Isoneurothrips antennatus* Moulton	*Isoneurothrips fasciatus* Moulton	*Stulothrips trespinus* Moulton	*Haplothrips paumalui* Moulton	*Haplothrips goudeyi* (Frank.)	*Haplothrips meladeuca* Bagnall	*Haplothrips (Hindsiana) sakimurai* Moulton	*Haplothrips* sp.*	*Kentronothrips hawaiiensis* Moulton
1935:																				
24 July	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
31 July	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
8 Aug.	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.
14 Aug.	1 D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
22 Aug.	1 D	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
31 Aug.	1 D	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
	1 E	.	.	.	1	.	1	.	.	.	.	.	.	4	.	.	1	.	.	.
6 Sept.	1 D	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	1	.	.
	1 E	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.
12 Sept.	1 D	.	.	.	.	.	7	.	3	1	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	.	.	4	.	.	1	.	.	.	.	.	.	.	.	.	.
18 Sept.	1 D	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 E	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	1	.	.	.
27 Sept.	1 D	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	1	.	2
	1 E	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
4 Oct.	1 D	.	.	.	.	1	1	.	.	1	.	.	.	.	1	1	.	2	.	3
	1 E	.	.	.	.	1	1	.	.	3	.	.	.	.	.	1	1	.	.	.
11 Oct.	1 D	.	.	.	.	.	1	.	.	.	.	.	.	1	.	1	.	.	.	.
	1 E	.	.	.	.	.	1	.	1	.	.	.	.	2	.	.	1	1	.	3
18 Oct.	1 D	.	.	.	.	.	8	2	.	2	.	.	.	32	.	2	.	1	.	.
	1 E	.	.	1	.	.	5	1	.	1	.	.	1	16	.	.	1	3	.	1
25 Oct.	1 D	.	.	.	.	.	26	4	.	.	.	.	.	20	.	5	.	3	.	2
	1 E	.	.	.	.	.	8	.	.	1	.	.	.	11	.	2	.	1	.	.
1 Nov.	1 D	.	.	.	.	.	15	1	.	1	.	.	.	.	.	3	.	2	.	.
	1 E	.	.	1	.	.	28	6	.	1	.	.	.	.	.	3	.	2	.	3
8 Nov.	1 D	.	.	1	.	.	11	.	.	1	.	.	.	.	.	2	.	1	.	1
	1 E	.	.	.	.	.	15	.	.	2	.	.	.	.	.	.	.	3	.	1
22 Nov.	1 D	.	.	.	1	.	28	11	2	2	.	.	.	7	.	5	.	1	.	2
	1 E	1	.	1	2	.	37	16	.	2	.	.	.	8	.	6	.	5	.	1
29 Nov.	1 D	.	.	.	1	.	9	5	.	2	.	.	.	13	.	2	.	.	.	.
	1 E	.	.	.	.	.	6	.	.	.	.	.	.	8	.	2	.	3	.	1
6 Dec.	1 D	.	.	.	.	.	4	1	.	.	.	.	.	2	.	.	.	.	.	.
	1 E	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
13 Dec.	1 D	.	1	.	.	.	4	1	.	.	.	.	.	6	.	2	.	1	.	1
	1 E	.	.	.	.	.	2	.	.	.	1	.	.	3	.	.	.	2	.	.
20 Dec.	1 D	.	.	.	.	.	.	1	1	.	1	1	.	7	.	1	.	.	.	.
	1 E	.	.	.	.	.	2	.	.	.	.	.	.	6	.	.	.	1	.	.
30 Dec.	1 D	.	.	.	2	.	14	2	.	1	.	.	.	.	.	6	.	.	.	4
	1 E	.	1	.	.	.	11	3	3	1	.	.	.	1	.	7	.	1	.	5
1936:																				
3 Jan.	1 D	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	1
	1 E	.	.	.	.	.	2	.	.	1	.	.	.	.	.	1	.	.	.	.

* Further identification was impossible because of imperfect specimen.

these species occur with such regularity and in such numbers as to prove that thrips as a group are not similar to *Thrips tabaci* in habit and that many species fly freely and disperse in great numbers in wind currents. In the writer's view, the wind trap data indicate that *Thrips tabaci* is not normally a migratory species and that only a drastic interruption of its host plants over a considerable area would force a mass movement of the species. The occasional high incidence of yellow spot in localized areas in pineapple plantings is adequate evidence that movements of considerable proportions do sometimes take place.

5. Incidence of yellow spot disease in pineapple plants

These data were taken from two pineapple fields in places contiguous to Area 3 (Plate 10, 3 and 4), and it was on the windward margins of these pineapple fields that the wind traps already referred to were placed.

Field 1 (Plate 10, 3). In this field, the incidence of yellow spot was observed during both susceptible periods, namely, when the plants were small, and later, during the development of the fruit. In the first-named period, yellow spot was apparently confined to a small area near the field border (Plate 10, 3 D, E). In this area, counts of infested plants in the border showed a percentage infection of 7·12. Immediately to leeward the percentage dropped to 3·54 while further in the field infection was incidental. A count made in the border area contiguous to that already mentioned showed a percentage infection of 1·57. Disease in fruit is shown in Table 9. These counts covered an area of ten field blocks of which eight are shown in Plate 10. From the table it is seen that incidence of yellow spot was extremely low.

Field 2 (Plate 10, 4). This area was abnormal in that it fruited out of season; but for the purposes of this paper this was desirable, since it provided a susceptible period during the winter months at a time when field populations of thrips were low in that area.

During November, when fruit began to ripen, preliminary counts were made, 12 November 1935, in the three blocks (Plate 10, 4 A, B, C). Two cases were observed in block 4 A out of 5400 fruits counted, none in block 4 B out of 3600 counted, and five from block 4 C out of 3000 counted. Block 4 C was fruiting more freely than either of the others and on 19 November counts in this block showed eight infected cases out of 1041 ripe fruits examined and twelve out of 4200 green fruits. From that time on regular counts were made and these are shown in Table 10.

Although the percentage of infected plants was small, there was a significantly higher incidence in block 4 C. This is believed to be associated with the discing down of the old field 2 A which lies directly to windward of the area in block 4 C from which the counts were made. This may well be an example of the postulate made previously in this paper, namely, that drastic

Table 9. *Area* 3, *Kipapa, Oahu* (*Plate* 10, 3). *Incidence of yellow spot disease in fruit crowns*

A, Number of pineapple crowns examined;
B, Number diseased;
C, Percentage diseased as determined on the following dates:

	20 May 1935			5 June 1935			13 June 1935		
Block	A	B	C	A	B	C	A	B	C
3 A	1521	5	0·33				1503	7	0·47
3 B	2044	0	0	4050	5	0·12	4045	9	0·22
3 C	753	0	0	1824	1	0·05	1823	1	0·05
3 D	917	0	0	1807	0	0	1807	1	0·06
3 E	1467	4	0·27	2886	13	0·45	2873	16	0·56
3 F							2919	5	0·17
3 G							2215	0	0
3 H							3688	6	0·16
3 I*				2767	0	0	2767	1	0·04
3 J*				4071	1	0·02	4070	2	0·05
Total	6702	9	0·13	17405	20	0·11	27710	48	0·17

	1 July 1935			15 July 1935			29 July 1935		
Block	A	B	C	A	B	C	A	B	C
3 A	1449	2	0·14	1098	3	0·27	318	4	1·26
3 B	3999	1	0·03	3194	2	0·06	654	1	0·15
3 C	1805	5	0·28	1444	2	0·14	362	1	0·28
3 D	1804	6	0·33	1698	8	0·47	973	0	0
3 E	2773	12	0·43	2241	11	0·49	1352	3	0·22
3 F	2876	5	0·17	1891	5	0·26	708	1	0·14
3 G	2211	2	0·09	1953	2	0·10	781	0	0
3 H	3682	3	0·08	3300	2	0·06	1343	0	0
3 I*	2764	1	0·04	2256	0	0	1144	0	0
3 J*	4068	0	0	3933	0	0	1828	2	0·11
Total	27431	37	0·13	23008	35	0·15	9463	12	0·13

* Not shown in Plate 10.

Table 10. *Area* 3 (*Plate* 10, 4 A, B, C). *Yellow spot disease in crowns and fruits*

	Block 4 A			Block 4 B			Block 4 C		
		Diseased			Diseased			Diseased	
Date	Normal	Crown	Fruit	Normal	Crown	Fruit	Normal	Crown	Fruit
1935:									
2 Dec.							39	1	0
8 Dec.							57	41	2
23 Dec.	73	0	0	177	0	0	128	1	0
30 Dec.	115	0	0	250	0	1	221	4	12
1936:									
6 Jan.	241	0	0	1157	1	0	1576	7	23
9 Jan.							919	5	7
13 Jan.	563	0	0	1180	1	1	2313	12	11
Total	992	0	0	2764	2	2	5253	71	55

disturbance of the host plant areas are necessary before incidence of infection assumes economic proportions.

Before yellow spot became evident in the developing crowns and fruit it was observed that scattered *Emilia* plants growing between the pineapple rows were showing a high percentage of infection. Counts made on this and later dates are shown in Table 11.

Table 11. *Records from Area* 3 (*Plate* 10, 4 A, B, C). *Thrips infestation and disease in* Emilia *growing among pineapple plants*

Date 1935	No. of plants sampled	% plants infested	% plants diseased	Av. no. of thrips per plant	Notes
8 Oct.	15	100	86·66	4·06	Scattered well-developed plants growing among pineapples, Plate 10, 4 C
30 Oct.	84	11·90	33·33	0·15	Young plants among pineapple, Plate 10, 4 B
27 Nov.	143	2·79	2·09	0·03	Plate 10, 4 A
	311	14·79	15·43	0·22	Plate 10, 4 B
	114	9·64	16·66	0·11	Plate 10, 4 C

It is evident from these data as well as from general field observations that a considerable reservoir of virus may exist in the pineapple fields with little or no transfer to pineapple plants taking place. This is readily explainable on the difference in suitability of the two plants as thrips hosts. A few scattered wind-blown thrips would be sufficient to infest and infect the relatively small populations of *Emilia* present. Infestation of pineapple plants, however, does not occur except rarely and even then only for a short period during blossoming, the thrips' sojourn on pineapple being transient. This transient stay is sufficient to infect the pineapple if the insect is viruliferous and the plant susceptible. There is no evidence to indicate movement of thrips from pineapple to pineapple, nor is movement from undisturbed *Emilia* growing among pineapple to nearby pineapple plants likely. There is, furthermore, no correlation between *Thrips tabaci* populations on *Emilia* in the sampled areas and disease in nearby pineapple fields, probably for the same reason, that undisturbed *Emilia* is a favoured host from which movement does not normally occur.

Quantitative data of the kind presented in this paper measure population per unit but not the total number of units. Under conditions normally prevailing in Hawaii the number of units in any locality contiguous to pineapple fields is high and the average population per unit host plant seems to provide a fair index, therefore, of the status of *Thrips tabaci* populations on *Emilia* in any particular locality.

Incidence of yellow spot disease in pineapple plantings is evidently conditioned by a number of interrelated factors. The higher the population of *Thrips tabaci* per unit of *Emilia*, the higher the potential incidence, but the factors governing dispersal must be operating positively and the pineapple plants be susceptible at one and the same time if incidence of the disease in

pineapple plants is to assume economic proportions. It is conceivable, however, that a large total population of thrips might disperse from an area showing a low population per unit but a large number of units, if the area as a whole was disturbed. The introduction of a new factor into the complex, such as, for example, a thrips parasite, could only be expected to influence the single factor of unit population.

6. Summary

1. Populations of *Thrips tabaci* Lind. on *Emilia sonchifolia* DC. were recorded from four locations, and data on wind dispersal of thrips species in pineapple were recorded from one location on the Island of Oahu, Territory of Hawaii.

2. Population densities varied widely between locations but seasonal trends were the same at all four points with populations decidedly lower in the winter months. The percentage of disease in *Emilia* followed closely the percentage of plants that were thrips infested, indicating that once a colony of *Thrips tabaci* is established on *Emilia* there is little movement therefrom.

3. Diseased *Emilia* plants maintain higher populations of *Thrips tabaci* on the average than do healthy *Emilia*.

4. Wind trap data indicate that *Thrips tabaci* is not a migratory species. Most of the species caught attained their greatest incidence and numbers during the fall and winter months. Incidence of yellow spot disease in pineapple is not correlated with *Thrips tabaci* populations on *Emilia* in nearby areas. This is accounted for on the grounds that *Emilia* is a favoured host from which dispersal does not normally occur.

5. Cultivation of host plant areas and drought are two possible dispersal factors.

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FURTHER CHANGES IN THE BRECKLAND AVIFAUNA CAUSED BY AFFORESTATION

By DAVID LACK

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1. Introduction

In a previous paper (Lack, 1933) the changes in bird life resulting from the planting of the Breckland heaths with pine (mostly *Pinus sylvestris*) were described up to the eleventh year after planting. A further visit to the area from 10 to 20 June 1937, has extended the study to the fifteenth year after planting, while many more figures have been obtained for younger plantations. In addition, visits have been made in mid-winter and early August, in order to study the populations outside the breeding season. The present paper may also be regarded as an addition to the general paper on British woodland birds by Lack & Venables (1939), in which the influence of the height of trees could not be specially investigated. As in the case of the previous investigation, I am deeply indebted to the Forestry Commission (England and Wales) for permission to work in the Breckland forests.

2. Description of the areas

A brief description of the areas studied was given in the earlier paper; see also Watt (1937) for a recent description of the heathland vegetation. All that need be added here is that, after the eleventh year, where the young pines average some 12 to 14 ft. high, growth continues rapidly and steadily, so that the 15-year-old plantations average some 23 ft. high. About the thirteenth year, but varying locally, the Forestry Commission cut away the lowest branches of the trees, and from now on the trees begin to be thinned out.

The removal of the lower branches affects adversely some of the species typical of secondary growth. Cones first appear in 7- or 8-year-old trees, and are common in 14- and1 5-year-old plantations. This affects the crossbill, which has occurred outside the breeding season in a 14-year-old plantation.

3. Methods

The observer walked through the various plantations noting every individual of every species seen or heard; especially in the denser plantations, the ear was more valuable than the eye. For comparing the populations in the different types of plantations, the total number of individuals of each species in each type of plantation was calculated as a percentage of the total number of individuals of all species in that type of plantation. (Therefore the figures are only comparative, but this is all that is needed for demonstrating the changes in species composition. Complete censuses are quite impracticable in the denser plantations.) For example, in 10-year-old plantations 197 birds were counted, of which 77 were willow warblers, giving a figure of 39%. Table 1 gives the species composition of each type of plantation in the breeding season calculated in this way. At the foot of the table is also given the total number of individual birds counted; 4-, 12- and 15-year-old plantations are represented by smaller totals than the others, hence the percentages for these may be rather less reliable.

It was not thought necessary to publish the actual counts, since these can be assessed from the percentage figures and the total of all individuals counted. Nor was it thought necessary to give precise localities. All refer to well-grown plantations near Thetford, Brandon or Harling, close to the Norfolk-Suffolk border. Some Breckland plantations have grown exceptionally poorly. Some of these counts were given in the earlier paper, but such areas were not included in the present investigation, except that the 12-year-old plantation was unavoidably poor—no better one was available. Full counts and precise localities, which are of interest only to someone working in the district, are being deposited with the British Trust for Ornithology, at Oxford.

Table 1 gives a full list of the breeding species met in the plantations during the counts except for a few listed in Appendix 1. Game birds and birds of prey, which have been greatly influenced locally by man, and a few other species of uncertain distribution, were omitted. Appendix 2 gives a similar list of species omitted in making Table 2.

4. The breeding birds

These are summarized in Table 1. On the "brecks", which have close-cropped grass, many bare and stony areas and rabbit burrows, seven species breed. Wheatear and stock dove nest down rabbit holes, stone curlew, lapwing,

Table 2. *Species composition of bird populations in pine plantations in mid-winter*

The figures represent the percentage of the total bird population formed by each species in each habitat

Bird	Heath	Age of pines (no. of years after planting) 4–5	6–7	8–9	10–11	13–15
Skylark	14	4	.	.	.	.
Meadow pipit	32	17	.	.	.	.
Stonechat	8	9	.	.	.	.
Reed bunting	×	15	×	×	.	.
Yellow hammer	.	11	.	.	.	.
Wren	24	32	18	21	13	8
Dunnock or hedge sparrow	.	.	13	8	5	1
Blackbird	8	×	5	.	4	3
Song thrush	×	.	7	×	.	.
Coal tit	.	.	11	46	32	29
Goldcrest	.	.	9	13	29	45
Robin	.	.	.	3	×	3
Blue tit	.	.	×	8	9	12
Willow tit (*Parus atricapillus*)	.	.	.	2	.	.
Bullfinch (*Pyrrhula pyrrhula*)	.	×	.	.	.	.
Jay (*Garrulus glandarius*)	.	.	.	.	×	2
Tree creeper (*Certhia familiaris*)	.	.	.	.	.	×
Crossbill (*Loxia curvirostra*)	.	.	.	.	.	2
Mistle thrush (*Turdus viscivorus*)	8	4	.	.	.	.
Green woodpecker (*Picus viridis*)	5	4	.	.	.	.
Total no. of birds counted	63	47	44	128	114	203

Table 3. *Counts taken in August* 1938

N.B. The figures were too few for calculating the populations by the percentage method used for Tables 1 and 2, so that actual counts are given.

Bird	Age of pines (no. of years after planting) 5	7	9	11	12	15	16
Skylark	1	.	.	.	.	.	.
Meadow pipit	2	.	.	.	.	.	.
Stonechat	3	.	.	.	.	.	.
Yellow hammer	.	1	.	.	1	.	.
Wren	1	5	7	1	7	7	2
Dunnock	1	5	6	2	4	.	.
Whitethroat	1	.	.	.	1	.	.
Willow warbler	5	2	29	8	19	9	12
Blackbird	2	3	18	3	2	2	4
Song thrush	.	.	2	.	.	.	.
Chaffinch	.	.	.	.	.	.	1
Coal tit	.	5	6	12	23	9	32
Goldcrest	.	4	4	7	18	10	17
Robin	.	.	1	.	6	2	1
Blue tit	.	2	2	3	3	2	7
Turtle dove	.	.	.	1	8	3	2
Lesser redpoll	.	.	.	1	1	.	.
Ring dove	.	.	.	2	.	2	6
Willow tit	.	.	1	3	.	.	.
Jay	.	.	.	1	.	.	1
Mistle thrush	.	.	2	.	.	.	.
Green woodpecker	.	2	.	1	1	.	2
Linnet (*Carduelis cannabina*)	1	.	2	.	.	.	.
Tree sparrow (*Passer montanus*)	.	2	.	.	.	.	.
Long-tailed tit (*Aegithalos caudatus*)	.	.	.	.	.	.	1
Little owl (*Athene noctua*)	.	.	.	.	1	.	.

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Table 1. *Species composition of bird populations in pine plantations in the breeding season*

The figures represent the percentage of the total bird population formed by each species in each habitat

Bird	Breck	Heath	Age of pines (no. of years after planting) 4	5	6	7	8	9	10	11	12*	14	15
Stock dove (*Columba aenas*)	6	.	.	.	.	.	.	.	.	.	.	.	.
Wheatear (*Oenanthe oenanthe*)	25	2	.	×	.	.	.	.	.	.	.	.	.
Stone curlew (*Burhinus oedicnemus*)	17	×	.	.	.	.	.	.	.	.	.	.	.
Ringed plover (*Charadrius hiaticula*)	5	.	.	.	.	.	.	.	.	.	.	.	.
Lapwing (*Vanellus vanellus*)	24	×	.	.	.	.	.	.	.	.	.	.	.
Skylark (*Alauda arvensis*)	24	52	39	29	33	8	6	1	.	.	.	.	.
Meadow pipit (*Anthus pratensis*)	.	27	27	28	11	4	3	1	1	.	.	.	.
Yellow wagtail (*Motacilla flava*)	.	2	.	1	×	1	.	.	.	.	.	.	.
Whinchat (*Saxicola rubetra*)	.	9	7	14	8	6	5	×	.	.	.	.	.
Stonechat (*Saxicola torquata*)	.	5	13	5	2	1	1	1	.	.	.	.	.
Reed bunting (*Emberiza schoeniclus*)	.	×	5	.	.	.	.	1	.	.	.	.	.
Yellow hammer (*Emberiza citrinella*)	.	1	5	2	4	2	2	4	5	3	.	.	.
Wren (*Troglodytes troglodytes*)	.	1	.	2	4	7	6	7	13	9	10	11	2
Whitethroat (*Sylvia communis*)	.	1	.	5	5	9	13	5	6	3	14	1	3
Willow warbler (*Phylloscopus trochilus*)	.	.	5	15	28	47	43	50	39	45	44	16	20
Grasshopper warbler (*Locustella naevia*)	.	.	.	.	×	.	.	.	.	.	.	.	.
Dunnock (*Prunella modularis*)	.	.	.	.	×	7	8	6	5	10	5	5	3
Blackbird (*Turdus merula*)	.	.	.	.	1	4	6	8	9	7	3	9	12
Song thrush (*Turdus ericetorum*)	.	.	.	.	.	×	×	3	8	2	.	1	2
Chaffinch (*Fringilla coelebs*)	.	.	.	.	.	1	4	9	11	10	15	34	28
Coal tit (*Parus ater*)	.	.	.	.	.	1	1	1	.	4	5	8	8
Goldcrest (*Regulus regulus*)	.	.	.	.	.	.	×	2	1	4	2	5	10
Robin (*Erithacus rubecula*)	.	.	.	.	.	.	×	×	.	1	.	5	3
Blue tit (*Parus caeruleus*)	.	.	.	.	.	.	.	×	.	×	.	×	.
Sedge warbler (*Acrocephalus schoenobaenus*)	.	.	.	.	.	.	.	×	.	×	.	.	.
Redstart (*Phoenicurus phoenicurus*)	.	.	.	.	.	.	.	.	1	.	.	.	.
Turtle dove (*Streptopelia turtur*)	.	.	.	.	.	.	.	.	1	×	.	×	×
Nightingale (*Luscinia megarhyncha*)	.	.	.	.	.	.	.	.	.	×	.	.	.
Lesser redpoll (*Carduelis flammea*)	.	.	.	.	.	.	.	.	.	×	.	.	.
Chiffchaff (*Phylloscopus collybita*)	.	.	.	.	.	.	.	.	.	.	.	2	.
Garden warbler (*Sylvia borin*)	.	.	.	.	.	.	.	.	.	.	2	.	.
Blackcap (*Sylvia atricapilla*)	.	.	.	.	.	.	.	.	.	.	.	1	7
Ring dove (*Columba palumbus*)	.	.	.	.	.	.	.	.	.	.	.	×	.
Tree pipit (*Anthus trivialis*)	.	×	.	×	.	.	.	.	.	.	.	.	×
Wood lark (*Lullula arborea*)	×	×	×	.	.	.	.	.	.	.	.	.	.
Total no. of birds counted	119	241	56	125	141	139	155	339	197	237	59	133	60
No. of different localities counted	3	3	2	3	4	3	2	5	2	4	1	1	1

* The 12-year-old plantation was more poorly grown than is typical.

skylark, red-legged partridge and locally the ringed plover, nest on the bare ground. Preparatory to planting with pines, rabbits are cleared and the burrows are filled in, while the grass grows taller. The bird population of such areas is not dissimilar to that of the natural heaths of the area, on which planting also occurs. On the heaths, which contain a variable proportion of *Calluna*, grasses (*Agrostis*, *Festuca*) and bracken (*Pteridium*), most of the bare "breck" species (wheatear, stock dove, stone curlew, lapwing, ringed plover) are very local. The skylark remains common, the meadow pipit is also common; and common partridge and, locally, yellow wagtail, also appear. Where the heath vegetation is taller, stonechat and whinchat colonize. These two vary similarly with regard to height of vegetation, but the former is mainly on *Calluna* and the latter mainly on grass heath. This difference accounts for their rather erratic distributions in Table 1.

The bird population of well-grown heaths is unaffected by pine plantations under four years old. After this, skylark and meadow pipit decrease rapidly, disappearing about the ninth year. Stonechat and whinchat, which are "scrub" species, increase in the fourth and fifth year, but then decrease. The willow warbler first appears in the fourth year, rapidly increases, and is the commonest species from the seventh to twelfth year, after which it declines in importance. Whitethroat and wren, which are occasional in tall, thick, heathland, become moderately common from the fifth to the twelfth year, but decrease when the lower branches of the pines are cut. The dunnock, another species characteristic of the secondary growth of woods, shows a very similar distribution, but first colonizes rather later.

Blackbird and song thrush colonize in the sixth and seventh years respectively. The latter is only local, but the former is characteristic of older plantations, and seems to be still increasing. The chaffinch, which first appears in the seventh year, becomes the commonest species in the fourteenth and fifteenth years. (It is the commonest bird in mature pine woods.) Two other characteristic pine wood birds, coal tit and goldcrest, colonize about the same time as the chaffinch, and are gradually increasing. The robin may also be increasing, but is as yet local. Finally, the ring dove has colonized the 14- and 15-year-old plantations.

In addition to these, various other species have bred occasionally (see Table 1). Of special interest are tree pipit and wood lark, which are driven from the heaths and brecks by the plantations, but return in the fourteenth or fifteenth year. Their typical habitat is heathland with a few tall trees. They disappear when the heathland is replaced by young pines, even when a few tall trees have been left, but return when the young plantations are tall enough to act as song posts, and nest in the heath vegetation provided by the rides and forest edges. One other species driven out by the planting will also return, but not till considerably later. The stock dove breeds in holes in rabbit burrows on the brecks and also in old trees.

Lack & Venables (1939) describe the avifauna of older pine plantations. From comparison with this it can be seen that by the fifteenth year a number of species characteristic of older plantations have still not colonized, especially such as the tree creeper and various tits and woodpeckers, which require holes or ledges in old trees for nesting, and such as various birds of prey, which nest high in the trees. Most other pinewood species found in eastern England have now colonized.

The rapidity and steadiness of the changes in the avifauna, correlated almost entirely with increasing height of the trees, are remarkable, and provide an almost unique example of an ornithological succession. Since huge areas of the Breckland have now been planted, one wonders where this enormous number of colonizing birds has come from, and where the dispossessed heathland birds have moved to.

5. Winter distributions

Counts were taken between 26 and 29 December 1936, and between 15 and 19 December 1937. Owing to the smaller totals involved, the results of Table 2 are calculated for 2-year groups. The total density of the bird populations in the plantations is considerably lower in winter than summer. Some species, such as the tits and goldcrest, tend to collect in foraging parties, and the occurrence of such large, but irregularly distributed, parties makes the figures less uniform than in the breeding season.

In the winter, summer visitors to England, such as the warblers and the whinchat, are of course absent. Skylark, meadow pipit and stonechat frequent the same habitats as in the breeding season but leave the plantations at a younger age, while the stonechat also spreads on to low heathland. The wren is more abundant, and spreads on to the heaths, where it does not breed. Dunnock, robin and blackbird remain about the same save that the blackbird also feeds on the heaths, where it does not nest. Goldcrest, coal and blue tits show a marked increase, especially the two tits, and occur in rather younger plantations than in the summer. The chaffinch and ring dove leave the plantations completely. Jay, tree creeper and crossbill, three birds which breed only in plantations rather older than those yet found in the Breckland forest, occur in the older plantations out of the breeding season. A few other species occur occasionally, as can be seen from Table 2.

No winter counts were taken on the bare brecks, which have a small population rather similar to that of cultivated land, with flocks of lapwing, starling and various Turdidae. The green woodpecker also feeds here, and on the heaths, but never far from trees, to which it retires if disturbed.

Table 2 shows that there is a succession of different species in winter as there is in summer, but fewer species are involved, so the results are less striking.

6. Late summer distributions

Counts were also taken between 9 and 12 August 1938. The data were not sufficient for percentage tabulations, so the actual counts are given in Table 3. By this date some species have already taken up their winter distributions. Thus all save one chaffinch had already left the plantations, the coal tit, blue tit and goldcrest were already in large foraging parties and were spreading into younger plantations. These foraging parties were also joined by willow warblers, many of which had not yet departed, and an occasional dunnock, whitethroat, robin, chaffinch, and other tits. No other points need special comment. A few species were recorded occasionally which have not been recorded at the other seasons (see Appendix 1).

(Small parties up to eight chaffinches, and larger flocks of tree sparrows, were seen in certain 5- and 6-year-old plantations in late June 1937. These birds were definitely not breeding there, but had moved in from elsewhere; all save an occasional tree sparrow had left by early August.)

7. Birds of the rides

Wide rides have been left in most plantations. These usually possess a typical heathland vegetation, and are frequented in small numbers by typical heathland birds, notably skylark, meadow pipit, stonechat, stone curlew, common and red-legged partridges, while various Turdidae and the green woodpecker feed there. The occurrence of tree pipit and wood lark has also been mentioned. Save for the two last, which depend also on the adjoining plantations, the birds of the rides were omitted from the counts of the plantations.

8. Comparison with other areas

Schiermann (1934) has made a comparable study of the breeding birds of the pine plantations in North Germany, in less detail for the younger plantations, but including more data from older plantations than those yet found on the Breck, and he has also worked out total densities. Schiermann's data show that the growth of the pines in his area is closely similar to that on the Breck, and a comparison of the birds which breed in both areas shows that their distributions with regard to height of trees are extremely similar in most cases. The similar distributions do not require comment, but two species are strikingly different. The chaffinch colonizes the Breckland plantations in the ninth year, the North German plantations not until the twentieth year; and the coal tit colonizes the Breckland plantations in the eleventh year, the North German plantations not until the thirty-fifth year. Possibly the German coal tits nest only in holes in trees and not also in holes in the ground as British coal tits do, for this latter habit alone makes possible the colonization of such young plantations.[1] The chaffinch uses trees for song posts and for

[1] This seems more likely to be due to an absence of holes in the ground in the German plantations than to a difference in the habits of the birds.

nesting, but it is quite unknown why the German birds should need so much higher trees for this purpose than the Breckland birds.

It had been hoped to compare the Breckland populations with other afforested areas in Britain, but none of those so far visited have proved suitable. Usually the plantations are not sufficiently extensive to get large enough counts, and in many cases the growth of the trees has been far less uniform than on the Breckland, which seems to offer specially favourable conditions. In the extensive plantations on the Culbin sands, Moray Firth, Scotland, the trees have grown much less regularly, and in general seem about four years behind those of the same age on the Breckland. A brief visit here in mid-April 1938 showed that the distributions of species common to both areas were similar (including, incidentally, chaffinch and coal tit) provided that the trees were compared by height and not by age.

9. Factors influencing distribution

The following discussion is not intended to be exhaustive, and many species of which little is known or which were discussed in the earlier paper are omitted. Knowledge of the earlier paper and of the general discussion of factors on a psychological plane in Lack (1937) is here assumed.

(*a*) *Species which colonize*

The absence of the *meadow pipit* from bare brecks, and its abundance on the heaths, seem correlated with its nest site in thick ground vegetation, which is not supplied by the brecks; for it regularly feeds on bare ground and sings in the air. Nest sites also seem to limit *yellow wagtail* and *common partridge*, which are also absent from the brecks but regular on the heaths.

The *stonechat* colonizes the taller heath vegetation and the young plantations. Outside the breeding season it is regular in low heathland, and it regularly feeds on the ground and in the air, and nests in thick ground vegetation. It normally sings from a perch several feet off the ground, and this seems the chief factor supplied by the young plantations; see also Lack & Venables (1939). Song posts also seem the limiting factor for the *whinchat* and *willow warbler*; the latter, for which thick cover may also be important, is discussed in the earlier paper.

The *wren* breeds on the tallest heaths and in the young plantations, and since it is regular on low heaths outside the breeding season, it is presumably limited by a breeding factor, but more is not known. The *dunnock* shows a rather similar distribution but does not spread on to low heathland in winter, hence a breeding factor cannot be all that is involved. The dunnock and also the *whitethroat* sing several feet off the ground, nest in thick cover off the ground and in general frequent thick cover, all of which are first supplied about the fifth year after planting.

The appearance of the *blackbird* in the sixth or seventh year seems primarily correlated with its song post, for it feeds mainly on the ground. Nest sites may be a subsidiary factor, for the typical site is a few feet off the ground, but lower forks, and also the ground, are used at times. The appearance of the *robin* also seems correlated with its song post, for it nests on the ground, feeds regularly on the ground and in general seems "at home" in low cover, but it sings fairly high up. Most species only limited by song posts spread into lower vegetation in autumn and winter; the robin does not do this, but, unlike most species, it maintains a territory with song in autumn and winter. The *chiffchaff* is also limited by its song post, for it nests only a few feet off the ground, feeds regularly in lower vegetation, but sings high up; it does not colonize until the fourteenth year. The song post limitations of *tree pipit* and *wood lark* have been discussed.

So soon as breeding is over, the *coal tit* spreads into much lower plantations, showing that its summer distribution is limited by a breeding factor, and since it nests on the ground, feeds in lower plantations, but sings high up, its song post is clearly indicated. The winter distribution of the *blue tit* is similar to that of the coal tit, but it does not breed in the 12- to 15-year-old plantations where the coal tit breeds; observation shows that its song post requirements would be met here, and its nest site is clearly the limiting factor, for, unlike the coal tit, it does not nest in holes in the ground, but only in holes off the ground. The distribution of the *goldcrest* both in summer and winter is similar to that of the coal tit, hence its summer distribution is clearly limited by a breeding factor; both song post and nest site are typically high off the ground. Since it occurs in younger plantations so soon as breeding is over, nest site and/or song post, both of which are typically high off the ground, would also seem to limit the *chaffinch*. The appearance of the *ring dove* in the fourteenth year seems probably associated with its nest site; it feeds outside the plantations. The occurrence of the *pheasant* in the plantations, but not usually on the heaths, is perhaps associated with its habit of roosting in trees, for it both nests and feeds on the ground; general cover may also be important.

Hence most of the arrivals which can be analysed seem correlated with nest site or song post. The song post assumes a far greater importance here than it would in a general discussion of the limits to bird distribution; but this is to be expected, since the changes in distribution are primarily correlated with the height, not the nature, of the vegetation.

(*b*) *Species which depart*

The departures are much harder to analyse than the arrivals. Those of *wheatear* and *stock dove* are clearly associated with the disappearance of the rabbit burrows in which they nest. Nest sites are clearly not involved in the

departure of *skylark*, *meadow pipit*, *whinchat* and *stonechat*, for an adequate number of sites remains in the older plantations. Food may be important for the skylark, which eats many seeds, but the other three species have a most varied insect diet. Whitethroat and dunnock decrease markedly in the older plantations so soon as the lower branches of the pines are cut; their song posts are still present, the insect life of the pines is still present, and their nest sites are still present, though only much higher off the ground. No direct environmental factor seems to prevent whitethroat and dunnock living in the "upper storey" of the older plantations, which seems to provide conditions extremely similar to those of younger plantations. But it is the habit of both species to frequent secondary growth close to the ground, and this habit seems the important factor. However, the evidence for this general habitat selection is less clear in such cases than in others discussed in the earlier papers.

10. Summary

1. Detailed figures from walking counts are given, comparing the successive breeding and mid-winter bird populations of Breckland heaths and pine plantations from 4 to 15 years old. Both in summer and winter, the changes in the populations resulting from the increasing height of the trees are extremely striking.

2. Comparison with Schiermann's data for North German pine plantations reveals many similarities in distribution, but chaffinch and coal tit colonize the British plantations much earlier than they do the German ones.

3. The factors limiting distribution are discussed. For colonizing species, song posts and to a less extent nest sites are the most important factors.

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Appendix 1. Species omitted from Table 1 of breeding bird populations

A few species were omitted from the calculated percentages of breeding bird populations, as their occurrences were too uncertain, or (game birds and birds of prey) were greatly influenced locally by human activities. The cuckoo

(*Cuculus canorus*) is regular on the heaths in small numbers, and was occasionally seen in older plantations; several species regularly parasitized by the cuckoo breed in the plantations, but it is not known if the cuckoo actually parasitizes them there. The nightjar (*Caprimulgus europaeus*), being crepuscular, was seldom observed; it was found in a 6- and an 8-year-old plantation and is regular on some of the heaths. The mistle thrush (*Turdus viscivorus*) was common in mid-June in plantations of most ages, especially in the rides. It is not known whether it breeds regularly, since nesting is over before the season when the counts were taken. An extremely young fledgling found in a 12-year-old plantation had almost certainly come from a nest in this plantation. The short-eared owl (*Asio flammeus*) and Montagu's harrier (*Circus pygargus*) have bred in some years in plantations up to 8 years old. (The marsh tit (*Parus palustris*) recorded from an 8-year-old plantation in 1931 was an error for coal tit (*P. ater*).) The pheasant (*Phasianus colchicus*) is regular in plantations of 4 years old up to 15 years old. The red-legged partridge (*Alectoris rufa*) is regular on the bare brecks, the heaths and plantations up to about 5 years old; after that it occurs in plantations only in the rides. Similar remarks apply to the common partridge (*Perdix perdix*) save that it is absent from bare brecks.

Appendix 2. Species omitted from Table 2 of winter bird populations

For similar reasons, various species were omitted from the percentage calculations for the mid-winter bird populations. The pheasant and the two partridges are distributed much as in the breeding season except that the pheasant is also regular on the heaths. Merlin (*Falco columbarius*), hen harrier (*Circus cyaneus*), sparrowhawk (*Accipiter nisus*) and other species of birds of prey at times hunt over the heaths and plantations. Carrion crow (*Corvus corone*), hooded crow (*C. cornix*), rook (*C. frugilegus*) and starling (*Sturnus vulgaris*) at times feed on the heaths and plantations up to 5 years old, the rook and starling being in flocks. Four goldfinches (*Carduelis carduelis*) were seen in a 5-year-old plantation; they also occurred on the very edges of other plantations. The list of casual winter visitors could be greatly extended, but the object of the present paper is to describe the distributions of the characteristic species.

THE BIRD POPULATION ON AN OXFORDSHIRE FARM[1]

By W. M. M. CHAPMAN

1. Place and times of censuses

The observations upon which this paper is based were made by members of the Oxford Ornithological Society on Temple Farm, Sandford-on-Thames, between 1926 and 1935. A census of the bird population on a typical piece of Oxfordshire farm land was originally suggested by Mr E. M. Nicholson; from 1930 onwards it was generally supervised by Mr W. B. Alexander (now Director of the Edward Grey Institute of Field Ornithology). This report has enjoyed the same supervision. In 1932 Mr Alexander published an account of the results obtained on the eastern half of this farm up to 1931 ("The bird population on an Oxfordshire farm", *J. Anim. Ecol.* (1932), 1: 58–64). The paper dealt primarily with the winter counts, those for the summer on the same area being given for comparison. In the four succeeding winters counts were made much more frequently and regularly, and it became evident that the conclusions based on the comparatively infrequent counts in the earlier winters were partly unreliable. This paper is therefore based on the results obtained in the later work (1931–5) and partly supersedes the earlier report with the same title.

Temple Farm consists (or consisted, some of it has since been built over) of some 300 acres of low level fields, lying on the left bank of the River Thames 3 miles below Oxford; it is roughly bisected by the Oxford-Henley road. The winter counts of 1926–7 to 1930–1 and 1934–5 were taken on 125 acres east of the road, consisting of pasture (except for small patches of stubble and clover in the first year or two), divided by hedges of varying height and density (2·7 miles per 100 acres) all containing oak (*Quercus*) and, predominantly, elm (*Ulmus*) trees. The eastern half includes a dry 4 acre copse, and about 8 acres of whins (*Ulex*). The winter counts of 1931–2 to 1933–4 were taken on an equal area (125 acres) west of the road. Of this about two thirds was pasture of the same type (only the fields are smaller, 3·1 miles of hedge per 100 acres), the remainder a large arable field with cottages along one side (1·25 miles of hedge per 100 acres). The western half includes two small copses totalling rather less than 1 acre. The summer counts of 1931–4 were taken on the eastern half as described; on a further 11 acres of pasture; on the western half as described, and on the water-meadows (including a wet copse) lying between the western half and the Thames. The summer area may be analysed as follows:

225 acres of pasture (8 acres of whins, 5 acres of dry copses, 6 miles of hedge).

[1] Publication of the British Trust for Ornithology.

40 acres of arable ($\frac{1}{2}$ mile of hedge).

32 acres of water-meadows (3 acres of wet copse, 1 mile of hedge, $\frac{1}{3}$ mile of river bank).

Total 297 acres: a good sample of mixed farm land with about $2\frac{1}{2}$ miles of hedge per 100 acres.

2. Validity of the sample censuses

This is an account of what was observed on one area, for what it is worth; if comparable observations can be made on other areas, they will, together, be worth much more. In the hope that such observations may be made, and may be comparable, I have given below some account of our procedure. The validity of a sample census depends upon three factors: (1) the size of the sample; (2) the methods by which figures are obtained; and (3) how these figures are handled.

(1) The size of a sample is measured in two ways. The *extension* of this census was small, in winter only 125 acres: its *intensity* was high; the last column in Table 2 is based on 86 counts spread over 10 winters. It was therefore in some sense equivalent to a single count of more than 20 square miles. We do not know what is the minimum sample area which yields any valid figures in a reasonable number of counts; it must, at any rate, include in the right proportions all the types of habitat in the area to be sampled. Nor do we know what is the largest area which it would be economical to survey; this depends on the range of the "chance" wanderings of the birds "resident" in the area. In practice, as large an area should be taken as can be adequately covered at one time. If this were found to be 60 acres of the kind of ground which I have described, and if it were possible to take 16 counts, I should be inclined, *ceteris paribus*, to take 8 counts of each of two adjacent and apparently homogeneous pieces of ground (taking precautions against counting the birds in, e.g. their common hedge, 16 times); if only 10 counts could be made, I should devote them all to one 60 acre piece. Our experience does not allow us to formulate more precise or more general rules for planning a census: it may be worth while to have indicated such rough conclusions as have been reached.

(2) *Methods.* In winter the ground was covered between 2 and 4 p.m. by a party of 6–12 observers. Their procedure was exactly that of a shooting party intent upon walking up partridges and beating the hedges for pheasants. Open fields were covered "in line", hedges taken with one observer on each side, copses "driven" (as by armed beaters who wanted their share of the shooting; birds were counted by observers both inside and outside the copse). The same route was always adopted and conferences held periodically to ensure that a blackbird, e.g. flying from one hedge to another (whether spontaneously or under provocation), had not been counted twice. The general impression was that the error was not more than 10%, and that birds counted

twice roughly balanced birds missed, though, for example, a blackbird is more likely to be counted twice, a tree-creeper to be missed. In a large number of counts an error of $\mp 10\%$ would disappear. The numbers of birds observed were entered field by field, and a record kept of the amount of hedge attributed to each field; this makes it possible in a later year to take a comparable census of *part* of the area. It was found that there was a limit to the usefulness of enduring wind and weather, for the birds didn't. It is not thought the errors caused by wrong identification were large.

The method employed in summer counts was to enter upon a map all birds apparently resident on the farm, with notes on their behaviour. This method was pursued with varying thoroughness. In 1931 the ground was only covered once. (The extra 11 acres on the east and the 40 acres arable on the west were not covered at all; averages from the other three years are inserted in the tables.) In 1932–3 it was covered twice. In 1934 an attempt was made to see whether a much more thorough survey would not yield very different figures. The area was divided into 9 small pieces and each surveyed on one or more afternoons in the 2nd, 4th, 6th and 8th weeks of University term (April–June), by the same two observers. A certain amount of checking was also done by supernumeraries. Great attention was given to the finding of nests. All observations were entered (in four coloured inks) on a map of the whole area (25 in. to 1 mile for fields, 50 in. to 1 mile for copses) from which the number of each species present was computed. So far as the commoner species are concerned, the percentage error, in an enquiry necessarily inexact, is almost certainly negligible. The figures thus obtained are reassuringly like those obtained in the three previous summers, though those for 1931 may not be very accurate. In particular the figure for song thrush is almost certainly too low. The economical method of 1932–3 (two counts, no insistence on finding nests) seems confirmed as adequate for our purpose. This does not apply to the copses, to which particular attention was given. There is something to be said for making a recount of any given area within a fortnight, but if both the early thrushes and the later warblers are to be observed this would involve four counts.

It may be worth while to give examples of the signs employed in mapping the farm in summer:

Bird apparently resident	• robin
with sex if possible	• blackbird ♂
if a bird of the year	• robin *Y*
singing cock	• wren ♂ *S*
with nesting material, food, excrement	• wren *B*, *F*, excrement
nest	× (robin)
with any contents	× (robin) 3 *E*, 1 *Y*,

this denotes a nest identified by build, eggs, or nestlings; a nest with a bird

in attendance is marked " ×chaffinch ♀ (or ♂)"; where the sex of this bird is indeterminate ♀ was assumed. This assumption was merely for marking purposes, to avoid the ambiguous mark " ×robin" (was there a bird there or does this belong to the pair seen 60 yd. × farther on?). This ambiguous sign should never occur.

Both summer (with one improper exception noted below) and winter tables take account of all birds "resident" on the area, including, for example, the hovering kestrel, but not of birds seen merely flying over (as distinct from about) the farm.

(3) The summer figures raise no problems of statistical method; we are dealing, more than less at any rate, with actual numbers of birds living on our area during the nesting season. But any winter population figure must be an average; upon how many counts should such averages be based? From a study of the figures at our disposal three conclusions seem to emerge: (*a*) In view of the fluctuations from month to month a series of six monthly averages gives a much better account of the bird population in any given winter than a single winter population average. (*b*) In view of what may be called "chance" fluctuations from count to count, an average figure for any month must be based on not less than 3 counts taken in the course of that month. The figures for the western half in 1933–4 show, I think, that a monthly average so based is reasonably valid. In this winter 4 counts a month were taken, averages based on any 3 counts do not in general greatly differ from those based on 4; averages based on any 2 counts differ very widely. The detailed figures on which this paper is based may be seen at the Edward Grey Institute. For the winters 1931–2–3 we have only 7 and 12 counts respectively; the populations of these winters can therefore only be described by single average winter population figures. (*c*) In view of both "chance" fluctuations, and fluctuations from month to month, any single winter population average should be based on, say, 2 counts a month, or at least on 9 counts taken at regular intervals. For the five winters 1926–7 to 1930–1 we have only 1, 4, 1, 7, 12 counts, taken at irregular intervals. On these records it does not seem justifiable to base more than one single winter population average for the "composite winter" 1926–31. This figure is a mean of monthly means based on the following numbers of counts: 5 Oct., 6 Nov., Dec. with 3 Jan., 8 Feb., 3 Mar.; the under-emphasis of Dec. and Jan., in 1933–4 the most populous period, may partly account for the low figure thus arrived at. (All the counts in these five winters were made on the eastern half.) From what has been said it follows that our averages must in all cases be means not medians.

The danger of accepting averages more narrowly based is well illustrated by certain figures (see Alexander, 1932) for the winters 1927–8, 1929–30, 1930–1. These figures lead almost irresistibly to two conclusions: (1) that the population is relatively constant in one winter and another; and (2) that the

fall in numbers during the winter (which we know must take place somewhere, whether or not there is a long period as well as an annual cycle in bird population) was observable to a very marked extent upon this area. More adequate observations now suggest: (1) that there are large and irregular fluctuations from one winter to another (Table 1); and (2) that no considerable decrease is observable on our area during the winter (Table 2). My own hypothesis is that this is a relatively sheltered spot, that the birds which die are, for the most part, those for which there is no room in such areas, and that the places of those which do die in such areas are rapidly filled.

My general conclusion of this section is that the figures given in the tables are reasonably valid: the sample big enough, the methods fairly accurate, the averages fairly well founded. I confess that I have applied no statistical controls, made no correlations, calculated no deviations; nor am I sure that this would be profitable. I do not think that more can be said than that the graphs of the tables are, upon the whole, less, not more erratic, than the impression received of the fluctuations in the bird population by the naturalist in the field. "To every enquiry its appropriate degree of exactitude" (Aristotle).

3. Discussion of the tables

The matter of this report lies not in the text but in the tables. Two general notes are required: (1) Numbers of birds observed (but not the number of times upon which a species was observed) are in all cases scaled to 100 acres; they are given (except in Table 3, part 3) to the nearest integer[1]; "1" denotes not $<0{\cdot}5$; "0", $<0{\cdot}5$; "–", total absence. The basis of each figure (i.e. the area covered and the number of counts) will be found in the tables or notes on them. (2) The way in which species are grouped is not that of any orthodoxy, though it nearly resembles that of the B.O.U.; it is the grouping into which the species seemed naturally to fall as we discussed their fluctuations in the field, and as I handled the figures recording these fluctuations.

Tables 1 *and* 2, *Winter*

Table 1 describes the only two winter populations of which we can give a full account, those of the western half in 1933–4, and of the eastern half in 1934–5. No account is taken, except in the totals, of species whose average was not 1 or more for one area and winter. I have no comments to make upon Table 1 that are not suggested by its perusal. The formation and dissolution of winter flocks (especially of skylarks and the finches) is well illustrated, and the steadiness of the "resident thrushes", dunnock and wren, and, in a lesser degree, tit groups, is clearly marked. The main difference between the two populations is the greater number of skylarks and finches on the western half, of which one-third was ploughed up; the dry copse on the eastern half accounts,

[1] Hence the *apparent* incorrectness of some of the figures in the totals and the summaries.

Table 1. *Winter populations* (*West:* 85 *acres pasture,* 40 *acres arable; East:* 125 *acres pasture*)

West, 1933–4	Times recorded out of 24	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Av.
Rook	**17**	4	2	19	14	2	1	7
Jackdaw	**4**	—	—	—	4	—	1	1
Starling	**24**	123	97	124	129	75	74	104
Chaffinch	**24**	22	32	18	20	11	29	22
House sparrow	**24**	78	50	27	19	21	20	35
Linnet	**12**	7	5	6	—	-	1	3
Greenfinch	**12**	0	1	0	1	2	1	1
Yellowhammer	**21**	23	17	10	14	0	30	16
Corn bunting	**11**	-	—	13	13	25	30	13
Skylark	**24**	23	32	50	54	63	17	40
Meadow pipit	**11**	2	3	2	5	2	3	3
Pied wagtail	**13**	1	2	1	0	2	0	1
Blue tit	**24**	4	8	6	11	10	12	8
Long-tailed tit	**14**	4	2	2	2	2	2	2
Great tit	**14**	1	1	0	1	0	2	1
Fieldfare	**16**	-	5	32	134	16	8	32
Redwing	**18**	—	7	29	17	25	11	15
Mistle thrush	**14**	-	2	3	2	1	0	1
Blackbird	**24**	25	25	25	23	23	25	24
Song thrush	**24**	13	12	13	13	10	8	11
Robin	**24**	10	10	8	5	9	7	8
Dunnock	**24**	2	4	3	4	3	5	3
Wren	**24**	4	3	3	2	4	4	3
Green woodpecker	**16**	1	0	2	0	1	1	1
Wood pigeon	**20**	2	1	0	2	3	4	2
Lapwing	**10**	4	7	0	1	1	4	3
Partridge	**20**	9	13	7	10	4	4	8
Summary								
Crows		4	2	19	18	2	2	8
Starling		123	97	124	129	75	74	104
Finches		108	88	51	40	34	50	61
Buntings		23	17	23	27	25	59	29
Lark, pipit, wagtail		26	37	53	60	67	20	44
Tits		9	10	8	15	12	16	12
Winter thrushes[1]		-	14	64	152	42	20	49
Resident thrushes[2]		47	47	46	41	42	41	44
Dunnock, wren		6	7	6	6	7	9	7
Non-passerine		16	21	9	14	9	13	14
Total (all species)		367	345	406	504	319	303	374

East, 1934–5	Times recorded out of 18	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Av.
Rook	**14**	2	0	1	23	2	12	7
Carrion crow	**13**	4	2	3	0	1	4	2
Jackdaw	**6**	1	—	—	6	—	2	2
Magpie	**15**	2	2	1	5	1	2	2
Jay	**13**	1	1	2	1	2	2	2
Starling	**18**	107	82	68	107	227	126	120
Chaffinch	**18**	9	8	21	21	10	9	13
House sparrow	**18**	16	19	40	15	12	14	19
Greenfinch	**17**	13	13	19	15	3	1	11
Goldfinch	**12**	6	1	4	1	2	2	2
Bullfinch	**12**	0	0	2	3	1	1	1
Yellowhammer	**17**	4	6	27	29	10	15	15
Skylark	**9**	3	0	1	11	2	—	3
Blue tit	**18**	5	6	8	6	6	5	6
Long-tailed tit	**15**	14	11	8	7	2	4	8
Great tit	**14**	1	1	1	3	1	1	2
Marsh tit	**11**	5	1	1	2	1	1	2
Fieldfare	**13**	5	18	80	27	59	8	33
Redwing	**10**	—	1	4	0	8	7	3
Blackbird	**18**	30	26	54	35	37	39	37
Song thrush	**18**	4	14	15	11	9	4	10
Robin	**18**	12	12	15	19	11	14	14
Dunnock	**18**	1	2	4	2	2	4	3
Wren	**18**	3	4	4	3	1	2	3
Green woodpecker	**16**	3	2	2	1	1	2	2
Wood pigeon	**14**	7	11	0	10	12	18	10
Lapwing	**4**	5	—	—	8	-	60	12
Partridge	**18**	9	9	23	17	9	8	13
Summary								
Crows		10	5	7	35	7	22	14
Starling		107	82	68	107	227	126	120
Finches		44	41	85	55	27	27	46
Buntings		4	6	27	29	10	15	15
Lark, pipit, wagtail		3	0	1	11	2	—	3
Tits		26	19	18	18	10	11	17
Winter thrushes[1]		5	19	84	27	68	15	36
Resident thrushes[2]		47	52	85	65	57	58	61
Dunnock, wren		5	6	8	5	4	6	6
Non-passerine		24	22	23	36	22	88	36
Total (all species)		280	255	410	394	437	373	360

[1] Including mistle thrush. [2] And robin.

Table 2. *Winter populations*

Part 1. Average numbers of commoner species

Index no.	Name	East, 125 acres pasture				West, 85 acres pasture					West, 40 acres arable					East and west pasture	
		1926–31 (25 counts)	1934–5 (18 counts)	Times recorded out of 43	Mean for 1926–31 and 1934–5	1931–2 (7 counts)	1932–3 (12 counts)	1933–4 (24 counts)	Times recorded out of 43	Mean for 1931–2–3–4	1931–2 (7 counts)	1932–3 (12 counts)	1933–4 (24 counts)	Times recorded out of 43	Mean for 1931–2–3–4	Times recorded out of 86	Mean of E. and W. (pasture)
1	Rook (*Corvus frugilegus*)	10	7	**26**	9	10	12	8	**29**	10	23	2	7	**12**	11	**55**	9
2	Carrion crow (*Corvus corone*)	1	2	**25**	2	1	2	1	**12**	1	3	5	0	**11**	2	**37**	1
3	Jackdaw (*Corvus monedula*)	0	2	**9**	1	1	0	1	**7**	1	2	0	0	**4**	1	**16**	1
4	Magpie (*Pica pica*)	0	2	**25**	1	—	0	1	**8**	0	—	—	—	**0**	—	**33**	1
5	Jay (*Garrulus glandarius*)	1	2	**24**	1	—	0	—	**1**	0	—	—	—	**0**	—	**25**	1
6	Starling (*Sturnus vulgaris*)	62	120	**38**	91	123	130	113	**42**	122	84	35	100	**38**	73	**80**	106
7	Chaffinch (*Fringilla coelebs*)	9	13	**43**	11	18	23	23	**43**	21	48	290	22	**42**	120	**86**	16
8	House sparrow (*Passer domesticus*)	1	19	**26**	10	63	23	31	**42**	39	140	45	48	**39**	78	**68**	25
9	Linnet (*Carduelis cannabina*)	6	1	**19**	3	5	3	4	**16**	4	150	138	3	**22**	97	**35**	4
10	Greenfinch (*Chloris chloris*)	5	11	**33**	8	5	2	2	**22**	3	1	8	0	**8**	3	**55**	5
11	Goldfinch (*Carduelis carduelis*)	2	2	**20**	2	6	2	1	**8**	3	—	1	1	**4**	1	**28**	3
12	Bullfinch (*Pyrrhula pyrrhula*)	1	1	**20**	1	1	0	1	**10**	0	—	—	0	**1**	0	**30**	1
13	Tree sparrow (*Passer montanus*)	0	0	**5**	0	0	—	—	**1**	0	1	3	0	**7**	1	**6**	0
14	Yellowhammer (*Emberiza citrinella*)	14	15	**35**	15	29	10	23	**38**	21	1	1	6	**14**	3	**73**	18
15	Corn bunting (*Emberiza calandra*)	0	0	**2**	0	—	—	20	**11**	7	—	—	3	**2**	1	**13**	3
16	Skylark (*Alauda arvensis*)	3	3	**17**	3	23	1	8	**26**	10	108	44	110	**41**	87	**43**	7
17	Meadow pipit (*Anthus pratensis*)	3	0	**18**	2	9	1	3	**17**	5	5	—	3	**8**	3	**35**	3
18	Pied wagtail (*Motacilla alba*)	0	0	**5**	0	—	0	—	**3**	0	2	—	3	**13**	2	**8**	0
19	Blue tit (*Parus caeruleus*)	4	6	**38**	5	13	10	11	**43**	11	7	5	5	**31**	5	**81**	8
20	Long-tailed tit (*Aegithalos caudatus*)	2	8	**25**	5	2	2	3	**20**	3	—	2	1	**5**	1	**45**	4
21	Great tit (*Parus major*)	2	2	**29**	2	5	4	1	**26**	3	2	3	1	**16**	2	**55**	2
22	Marsh tit (*Parus palustris*)	1	2	**18**	1	1	0	0	**7**	0	—	—	—	**0**	—	**25**	1
23	Tree-creeper (*Certhia familiaris*)	1	1	**15**	1	1	0	1	**10**	0	—	—	0	**2**	0	**25**	1
24	Fieldfare (*Turdus pilaris*)	7	33	**23**	20	34	21	48	**26**	34	18	1	5	**10**	8	**49**	27
25	Redwing (*Turdus musicus*)	2	3	**18**	3	13	4	20	**27**	12	4	5	7	**11**	5	**45**	8
26	Mistle thrush (*Turdus viscivorus*)	1	0	**12**	1	5	2	2	**25**	3	1	2	2	**12**	1	**37**	2
27	Blackbird (*Turdus merula*)	28	37	**43**	33	47	47	31	**43**	42	23	41	14	**42**	26	**86**	37
28	Song thrush (*Turdus ericetorum*)	6	10	**42**	8	33	17	14	**43**	22	14	26	7	**39**	16	**85**	15
29	Robin (*Erithacus rubecula*)	6	14	**43**	10	31	18	11	**43**	20	8	5	4	**38**	6	**86**	15
30	Dunnock (*Prunella modularis*)	2	3	**37**	2	3	5	4	**39**	4	2	2	2	**16**	2	**76**	3
31	Wren (*Troglodytes troglodytes*)	3	3	**41**	3	4	5	5	**41**	5	3	1	2	**15**	2	**82**	4
32	Green woodpecker (*Picus viridis*)	1	2	**30**	1	1	1	1	**25**	1	1	—	—	**1**	0	**55**	1
33	Lapwing (*Vanellus vanellus*)	7	12	**13**	10	6	3	2	**12**	4	18	21	4	**9**	14	**25**	7
34	Wood pigeon (*Columba palumbus*)	10	10	**32**	10	6	3	2	**34**	4	9	1	1	**13**	4	**66**	7
35	Stock dove (*Columba oenas*)	2	0	**7**	1	0	0	0	**3**	0	0	2	0	**2**	1	**10**	1
36	Partridge (*Perdix perdix*)	6	13	**41**	9	6	4	8	**30**	6	8	16	9	**18**	11	**71**	8
37	Species in Part 2	3	3	..	3	1	1	1	...	1	1	0	1	...	1	...	2

Part 2. Number of times on which uncommon species were recorded

38	Brambling (*Fringilla montifringilla*)	—	—	—	...	1	—	—	1	...	—	1	—	1	...	1	...
39	Reed bunting (*Emberiza schoeniclus*)	2	1	3	...	4	2	—	6	...	1	—	—	1	...	9	...
40	Cirl bunting (*Emberiza cirlus*)	—	—	—	...	—	—	1	1	...	—	—	—	—	...	1	...
41	Grey wagtail (*Motacilla cinerea*)	—	—	—	...	—	1	—	1	...	—	—	—	—	...	1	...
42	Cole tit (*Parus ater*)	1	—	1	...	—	—	2	2	...	—	—	—	—	...	3	...
43	Willow tit (*Parus atricapillus*)	?	?	?	...	—	—	—	—	...	—	—	—	—	...	?	...
44	Goldcrest (*Regulus regulus*)	4	2	6	...	—	2	—	2	...	—	—	—	—	...	8	...
45	Nuthatch (*Sitta europaea*)	—	—	—	...	—	—	1	1	...	—	—	—	—	...	1	...
46	Stonechat (*Saxicola torquata*)	4	1	5	...	—	—	—	—	...	—	—	—	—	...	5	...
47	Gr. sp. woodpecker (*Dryobates major*)	3	—	3	...	—	—	1	1	...	—	—	—	—	...	4	...
48	Lr. sp. woodpecker (*Dryobates minor*)	1	—	1	...	—	2	1	3	...	—	—	1	1	...	4	...
49	Barn owl (*Tyto alba*)	3	1	4	...	—	—	—	—	...	—	—	—	—	...	4	...
50	Tawny owl (*Strix aluco*)	1	7	8	...	—	—	2	2	...	—	—	—	—	...	10	...
51	Little owl (*Athene noctua*)	8	9	17	...	1	3	5	9	...	—	—	—	—	...	26	...
52	Peregrine (*Falco peregrinus*)	—	—	—	...	—	—	3	3	...	—	—	—	—	..	3	...
53	Kestrel (*Falco tinnunculus*)	8	8	16	...	1	1	4	6	...	—	1	2	3	...	22	...
54	Sparrow hawk (*Accipiter nisus*)	2	2	4	...	1	—	1	2	...	—	—	—	—	...	6	...
55	Mallard (*Anas platyrhynchus*)	5	2	7	...	—	—	—	—	...	—	—	1	1	...	7	...
56	Teal (*Querquedula crecca*)	—	2	2	...	—	—	—	—	...	—	—	—	—	...	2	...
57	Heron (*Ardea cinerea*)	1	1	2	...	—	1	3	4	...	—	—	1	1	...	6	...
58	Common snipe (*Capella gallinago*)	10	—	10	...	1	1	—	2	...	—	—	—	—	...	12	...
59	Jack snipe (*Lymnocryptes minimus*)	—	—	—	...	1	—	—	1	...	—	—	—	—	...	1	...
60	Domestic pigeons (*Pigeones domesticatae*)	—	—	—	...	—	—	—	—	...	—	—	4	4	...	0	...
61	Moorhen (*Gallinula chloropus*)	5	1	6	...	—	1	—	1	...	—	—	—	—	...	7	...
62	Pheasant (*Phasianus colchicus*)	14	10	24	...	1	2	1	4	...	—	—	—	—	...	28	...

Part 3. Summary

Crows (1–5)	12	14	...	13	12	14	10	...	12	26	7	7	...	13	...	13
Starling (6)	62	120	...	91	123	130	113	...	122	84	35	100	...	73	...	106
Finches (7–13, 38)	24	47	...	36	97	53	61	...	70	340	485	73	...	299	...	53
Buntings (14, 15, 39, 40)	14	15	...	15	29	10	43	...	27	1	1	8	...	3	...	21
Lark, pipit, wagtails (16–18, 41)	6	3	...	5	32	3	11	...	15	114	44	116	...	91	...	10
Tits, etc. (19–23, 42–45)	10	18	...	14	21	17	15	...	18	8	10	6	...	8	...	16
Winter thrushes (24–26)	11	37	...	24	52	28	69	...	50	22	7	14	...	15	...	37
Resident thrushes (27–29, 46)	39	61	...	51	111	82	56	...	83	44	72	24	...	47	...	67
Dunnock, wren (30, 31)	5	6	...	5	7	10	8	...	8	5	3	4	...	4	...	7
Non-passerine (32–36, 47–62)	28	39	...	34	21	11	15	...	16	36	39	15	...	30	...	25
Total all species (1–62)	212	360	...	286	504	357	401	...	421	681	702	369	...	584	...	354

in winter as in summer, for its higher figures for magpie, jay, bullfinch, owls, and wood-pigeon.

Table 2 compares single average winter population figures for five winters, two on the eastern half and three on the western half. The pasture and arable areas on the western half are treated separately. The first part of the table deals only, except in the last line, with species whose average on any one area (east, west pasture, west arable) in any one winter was 1 or more. The second part gives the *number of times* that other species were recorded. The third is a summary of the first (and so in its last line of the second[1]). The total pasture populations, if the not very satisfactory figure[2] in the first column be ignored, vary between 3·6 and 5·0 birds per acre. The total arable populations, which consist principally of large flocks of finches and skylarks, are rather higher, and are subject to rather greater fluctuation, 3·7–7·0 birds per acre. It will be seen that the species which in this table show relatively little fluctuation from year to year, are those which, in Table 1, show relatively little fluctuation from month to month. They are the hedge association, "resident thrushes", dunnock and wren, and the tits. Further, they are about equally numerous on pasture and on arable. For although their figures, calculated (as in Table 2) per 100 acres, are lower on arable; if calculated per mile of hedge they would be very similar. (The hedge per 100 acres attributed to the arable area is only about half that of the pasture.)

Table 3, *Summer*

Table 3 compares the populations of the whole farm in the four summers 1931–4. The first part deals (to the nearest integer) with all species whose mean figure for the four summers is 1 or more. The second gives (to the nearest tenth) the mean figures for the four summers of all other species recorded, and the number of summers in which they occurred. Though there are more species (31/58) these make up only 6% of the average total population. The third part is a summary of the first two, and takes account of the numbers in each year of the species dealt with in the second part.

I have worked out separate figures for the three types of ground into which the summer area is divided (pasture, arable, water-meadows; see introductory

[1] Or rather, of the unprinted fractional figures for the species dealt with in Part 2, corresponding with the figures in Part 1.

[2] It is almost certainly too low, see p. 289. The facts there given will not, indeed, account for the whole difference between the populations of the eastern half in 1926–31 and 1934–5. It is possible that the establishment of roosts of fieldfares and finches (mainly house sparrow) in the interval, may to some small extent account for the higher total of the later winter, for counts were taken in the afternoon and a certain number of fieldfares and finches may have been counted which were resident on the farm rather by night than by day. But this will not account for the general increase (see blackbird, robin, tits and other species). Nor are we able to assign any differences in weather or crops as the causes of similar increases and decreases on the western half in the winters 1932–3–4.

Table 3. *Summer populations*, 1931–4 (297 *acres*)

Part 1

Index no.	Name	1931	1932	1933	1934	Mean
1	Carrion crow (*Corvus corone*)	3	1	3	1	2
5	Starling (*Sturnus vulgaris*)	5	2	3	10	5
6	Chaffinch (*Fringilla coelebs*)	25	24	28	23	25
7	Linnet (*Carduelis cannabina*)	6	8	13	14	10
8	House sparrow (*Passer domesticus*)	4	5	11	10	7
9	Yellowhammer (*Emberiza citrinella*)	9	6	9	5	7
10	Greenfinch (*Chloris chloris*)	3	2	2	3	3
16	Skylark (*Alauda arvensis*)	5	1	3	4	3
17	Tree pipit (*Anthus trivialis*)	2	2	2	1	2
20	Blue tit (*Parus caeruleus*)	3	2	4	7	4
21	Long-tailed tit (*Aegithalos caudatus*)	2	1	2	4	2
22	Great tit (*Parus major*)	2	2	1	2	2
27	Whitethroat (*Sylvia communis*)	11	7	12	11	10
28	Lesser whitethroat (*Sylvia curruca*)	1	1	1	1	1
29	Garden warbler (*Sylvia borin*)	2	2	0	1	1
30	Willow wren (*Phylloscopus trochilus*)	4	3	1	4	3
31	Chiffchaff (*Phylloscopus collybita*)	4	2	2	2	2
35	Blackbird (*Turdus merula*)	37	36	41	42	39
36	Song thrush (*Turdus ericetorum*)	12	22	21	22	19
37	Robin (*Erithacus rubescens*)	12	10	12	8	11
38	Whinchat (*Saxicola rubetra*)	1	2	1	1	1
42	Dunnock (*Prunella modularis*)	7	6	8	7	7
43	Wren (*Troglodytes troglodytes*)	7	10	6	6	7
51	Lapwing (*Vanellus vanellus*)	1	3	5	6	4
53	Moorhen (*Gallinula chloropus*)	3	4	3	2	3
54	Wood pigeon (*Columba palumbus*)	9	3	5	9	6
57	Partridge (*Perdix perdix*)	1	0	2	2	1

Part 2

Index no.	Name	No. of summers in which present	Mean 1931–4
2	Jackdaw (*Corvus monedula*)	1	0·3
3	Magpie (*Pica pica*)	3	0·9
4	Jay (*Garrulus glandarius*)	3	0·4
11	Goldfinch (*Carduelis carduelis*)	2	0·3
12	Bullfinch (*Pyrrhula pyrrhula*)	2	0·3
13	Tree sparrow (*Passer montanus*)	2	0·6
14	Corn bunting (*Emberiza calandra*)	3	0·4
15	Reed bunting (*Emberiza schoeniclus*)	2	0·3
18	Pied wagtail (*Motacilla alba*)	1	0·1
19	Yellow wagtail (*Motacilla flava*)	1	0·1
23	Marsh tit (*Parus palustris*)	4	0·7
24	Willow tit (*Parus atricapillus*)	1	0·1
25	Cole tit (*Parus ater*)	2	0·3
26	Tree creeper (*Certhia familiaris*)	3	0·4
32	Spotted flycatcher (*Muscicapa striata*)	3	0·7
33	Blackcap (*Sylvia atricapilla*)	3	0·7
34	Sedge warbler (*Acrocephalus schoenobaenus*)	3	0·5
39	Mistle thrush (*Turdus viscivorus*)	4	0·8
40	Redstart (*Phoenicurus phoenicurus*)	1	0·3
41	Nightingale (*Luscinia megarhyncha*)	3	0·2
44	Green woodpecker (*Picus viridis*)	3	0·6
45	Cuckoo (*Cuculus canorus*)	3	0·4
46	Kingfisher (*Alcedo atthis*)	2	0·3
47	Tawny owl (*Strix aluco*)	2	0·3
48	Little owl (*Athene noctua*)	4	0·6
49	Kestrel (*Falco tinnunculus*)	2	0·3
50	Mallard (*Anas platyrhyncha*)	1	0·1
52	Snipe (*Capella gallinago*)	3	0·3
55	Stock dove (*Columba oenas*)	1	0·1
56	Turtle dove (*Streptopelia turtur*)	2	0·3
58	Pheasant (*Phasianus colchicus*)	2	0·3
	Total		12·0

Part 3

1–4	Crows	5	1	4	3	4
5	Starling	5	2	3	10	5
6–15	Finches, buntings	50	45	65	58	54
16–19	Lark, pipit, wagtails	6	3	5	5	5
20–26	Tits, creeper	10	7	8	14	10
27–34	Warblers	25	15	19	20	20
35–41	Thrushes	68	70	77	73	71
42–43	Dunnock, wren	14	16	14	13	14
44–58	Non-passerine	17	13	21	22	18
	Total (all species)	198	172	215	217	200

Part 3 is a summary of Parts 1 and 2 (i.e. it takes into account the annual figure not printed for species in Part 2). The figures in the "mean" columns have only to be divided by 2 to yield the percentage, for the species or group in question, of the total population.

section), but it is not worth while to print these details. It does indeed appear from them that the water-meadows were a little richer than the rest of the area, that the warblers (except whitethroat) were found in the copses, and the kingfisher's nest in the river bank. But no differences are found comparable to the difference between pasture and arable populations in winter. The summer population seems to be fairly evenly spread out and to depend rather on length and density of hedges (the copses are little more than grown-up hedges) than upon acreage. Much the most striking thing about summer population is the extremely close correlation between any two summers, its constancy.

One comment must be made: it may be taken from the absence of, for example, rook, that all passengers were excluded, for though rooks did not nest, they did, of course, feed on the farm. Such exclusion would clearly be improper; it is possible that a considerable proportion of the summer population may consist of non-breeding birds, stationary or wandering. In general any bird seen on the farm was marked down; those not seen again were counted, in 1934, for example, when 4 counts were made, as $\frac{1}{4}$. But rooks, and to a lesser extent, jackdaws, swifts, swallows, house martins and lapwings, which could be known not to be breeding, were in some years arbitrarily excluded. The omission of rook is not of any importance, for the number of counts made in summer could not be supposed to yield a valid average for a species visiting the farm irregularly in fairly large numbers. The rook census of 1931 gives the summer population for the Upper Thames area as 14 per 100 acres.

Tables 4 *and* 5, *Summer and Winter compared*

It may be worth while, if only to show how little correlation there is between them, to compare the populations on the same area in consecutive summers and winters. Table 4 is a comparison (not abstractable from the other tables printed) (*a*) of the eastern half (pasture) summer 1934 with the following winter; (*b*) of the western half, pasture, summers 1932, 1933, 1934, with the respectively previous winters; (*c*) of the western half, arable, mean summer population 1932–4 with mean winter population 1931–4. This last area seems too small, and the fluctuations in its population too large, to give more than a mean figure. It will be seen that on pasture the summer is a little more than half the total winter population. On arable the summer appears to be only a quarter of the winter population; but the arable area had only half as much hedge per 100 acre as the pasture. If I am right in thinking that arable winter population depends chiefly on acreage, and that summer population, on arable as on pasture, depends chiefly on the amount of hedge, then we may conclude that on arable with $2\frac{1}{2}$ miles of hedge per 100 acres the

Note: Except in the summaries of groups and the totals, no note is taken in Table 4 of species with figures less than 1 for the subdivisions of the area.

Table 4. *Summer and winter comparisons*

	East 125 acres pasture		West 85 acres pasture								West 40 acres arable	
	W. 1934–5	S. 1934	W. 1931–2	S. 1932	W. 1932–3	S. 1933	W. 1933–4	S. 1934	W. mean	S. mean	W. mean 1931–4	S. mean 1932–4
Carrion crow	2	**2**	1	—	2	**3**	1	—	1	**1**	2	—
Magpie	2	**5**	—	—	0	—	1	—	0	—	—	—
Jay	2	**2**	—	—	0	—	—	—	0	—	—	—
Starling	120	**7**	123	**5**	130	—	113	**21**	122	**9**	73	**4**
Chaffinch	13	**16**	18	**30**	23	**25**	23	**31**	21	**29**	120	**16**
House sparrow	19	**1**	63	—	23	**1**	31	**21**	39	**7**	78	**17**
Linnet	1	**11**	5	**16**	3	**19**	4	**23**	4	**19**	97	**9**
Greenfinch	11	**3**	5	**3**	2	**1**	2	**5**	3	**3**	3	**3**
Bullfinch	1	—	1	—	0	—	1	—	0	—	0	**2**
Goldfinch	2	—	6	—	2	—	1	—	3	—	1	—
Tree sparrow	0	**1**	0	—	—	—	—	—	0	—	1	—
Yellowhammer	15	**7**	29	**11**	10	**16**	23	**6**	21	**11**	3	**3**
Corn bunting	0	—	—	—	—	**1**	20	—	7	**0**	1	**2**
Reed bunting	0	**2**	0	—	0	—	—	—	0	—	0	—
Skylark	3	**3**	23	**4**	1	**8**	8	**10**	10	**7**	87	**2**
Meadow pipit	0	—	9	—	1	—	3	—	5	—	3	—
Tree pipit	—	**0**	—	**1**	—	—	—	—	—	**0**	—	—
Pied wagtail	0	—	—	—	0	—	—	—	0	—	2	—
Blue tit	6	**5**	13	**1**	10	**1**	11	**11**	11	**5**	5	**1**
Long-tailed tit	8	**4**	2	**1**	2	—	3	**3**	3	**1**	1	**3**
Great tit	2	**0**	5	**1**	4	**3**	1	**2**	3	**2**	2	**2**
Marsh tit	2	**0**	1	—	0	—	0	—	0	—	—	—
Willow tit	0	**1**	—	—	—	—	—	—	—	—	—	—
Tree creeper	1	—	1	—	0	—	1	**0**	0	**0**	0	**0**
Fieldfare	33	—	34	—	21	—	48	—	34	—	8	—
Redwing	3	—	13	—	4	—	20	—	12	—	5	—
Mistle thrush	0	—	5	**1**	2	—	2	**1**	3	**1**	1	**2**
Song thrush	10	**11**	33	**26**	17	**35**	14	**30**	22	**30**	16	**18**
Blackbird	37	**31**	47	**50**	47	**55**	31	**57**	42	**54**	26	**35**
Robin	14	**6**	33	**18**	18	**14**	11	**6**	20	**12**	6	**6**
Whinchat	—	**2**	—	—	—	—	—	—	—	—	—	—
Nightingale	—	**1**	—	—	—	—	—	—	—	—	—	—
Dunnock	3	**7**	3	**8**	5	**15**	4	**4**	4	**9**	2	**4**
Wren	3	**1**	4	**11**	5	**3**	5	**8**	5	**7**	2	**3**
Blackcap	—	**1**	—	—	—	—	—	—	—	—	—	—
Garden warbler	—	**2**	—	—	—	—	—	—	—	—	—	—
Willow wren	—	**4**	—	—	—	—	—	**3**	—	**1**	—	**2**
Chiffchaff	—	**2**	—	—	—	**1**	—	—	—	**0**	—	—
Whitethroat	—	**13**	—	**10**	—	**18**	—	**13**	—	**13**	—	**7**
Lesser whitethroat	—	**2**	—	**3**	—	—	—	—	—	**1**	—	—
Green woodpecker	2	**2**	1	—	1	—	1	—	1	—	0	—
Cuckoo	—	**0**	—	—	—	**1**	—	—	—	**0**	—	**1**
Little owl	0	**2**	0	**3**	0	**1**	0	—	0	**1**	—	—
Kestrel	0	**0**	0	**1**	0	—	0	—	0	**0**	0	—
Lapwing	12	**8**	6	**8**	3	**10**	2	**10**	4	**9**	14	—
Wood pigeon	10	**16**	6	**6**	3	**4**	2	**4**	4	**5**	4	**3**
Stock dove	0	—	0	—	0	—	0	**1**	0	**0**	1	—
Moorhen	0	—	—	**3**	0	**3**	—	—	0	**2**	0	—
Partridge	13	**3**	6	**1**	4	—	8	**1**	6	**1**	8	—
Pheasant	0	**2**	0	—	0	—	0	—	0	—	—	—
Summary												
Crows	7	**9**	2	—	2	**3**	2	—	2	**1**	2	—
Starling	120	**7**	123	**5**	130	—	113	**21**	122	**9**	73	**4**
Finches	47	**32**	97	**49**	53	**46**	61	**80**	70	**58**	299	**47**
Buntings	15	**9**	29	**11**	10	**17**	43	**6**	27	**11**	3	**5**
Lark, pipits, wagtail	3	**3**	32	**5**	3	**8**	11	**10**	15	**8**	91	**2**
Tits, creeper	18	**10**	21	**3**	17	**4**	15	**16**	18	**8**	8	**6**
Thrushes	98	**51**	163	**95**	110	**104**	125	**94**	133	**97**	62	**61**
Dunnock, wren	6	**8**	7	**19**	10	**18**	8	**12**	8	**16**	4	**7**
Warblers	—	**24**	—	**13**	—	**19**	—	**16**	—	**16**	—	**9**
Non-passerine	39	**33**	21	**22**	11	**19**	15	**16**	16	**19**	30	**4**
Total (all species)	353	**186**	494	**222**	345	**238**	393	**271**	411	**243**	573	**145**

proportion of winter to summer population would have been not very much higher than the proportion found on pasture, say 5 : 2.

Finally, if we consider the whole area covered in both summer and winter (that is, the summer area as described, less the water-meadows and 11 acres pasture on the east side), and if we quote as the "winter population" for this area a mean of the average winter population on the eastern half and the average winter population on the western half, we find that the numbers (of those species whose average summer or winter figure is 1 or more) compare as follows (Table 5). The source of the summer figure for rook is given above. The reader is reminded that figures are given per 100 acres and to the nearest integer; "0" denotes $<0{\cdot}5$.)

Table 5. *Comparison of average populations (per hundred acres) in winter and summer*

Species	Winter	Summer	Species	Winter	Summer
Fieldfare	23	—	Greenfinch	5	2
Meadow pipit	3	—	Long-tailed tit	4	2
Redwing	6	—	Dunnock (hedge sparrow)	3	7
Starling	98	5	Wren	3	5
Blackbird	35	36	Carrion crow	2	2
Chaffinch	32	21	Corn bunting	2	0
House sparrow	31	7	Great tit	2	1
Linnet	19	11	Goldfinch	2	0
Skylark	19	4	Mistle thrush	2	1
Yellowhammer	15	8	Green woodpecker	1	1
Song thrush	14	17	Jay	1	0
Robin	13	9	Magpie	1	1
Rook	10	14	Chiffchaff	—	1
Lapwing	8	5	Lesser whitethroat	—	1
Partridge	8	1	Whinchat	—	1
Blue tit	7	2	Whitethroat	—	11
Wood pigeon	7	6	Willow wren	—	2

4. Summary

Winter censuses of the bird population on areas of 125 acres in the Thames Valley near Oxford between 1926 and 1935 (86 counts) show the composition of the bird population and the limits within which it fluctuated. The species most regular from month to month, from winter to winter, and from pasture to arable land, were those dependent on the hedges; the least regular were the finches, found mainly in large flocks on arable. The total winter population varied, on pasture (2·7 miles of hedge per 100 acres) from 3·6 (omitting one record, for reasons given above) to 5·0 birds per acre; on arable from 3·7 to 7·0 birds per acre. (Throughout this paper "arable" means, of course, arable surrounded by pasture; on a purely arable area a very different population might be found.) Two tables showing the population month by month in single winters show rather the "chance" fluctuations of the "arable" species, and the formation and dissolution of winter flocks, than any decrease during the course of the winter.

Summer censuses of the bird population on about 300 acres of the same farm in 1931, 1932, 1933 and 1934 show the composition of the summer population and its constancy. It appears that in summer the regularity which in winter is found only in the hedge association is extended to almost all species. There was little variation from summer to summer, or from pasture to arable land. The average total population was 2 birds per acre.

A comparative table shows no correlation between the populations of consecutive summers and winters. On the average, on the same ground, the winter was roughly double the summer population.

THE NOCTURNAL ACTIVITY OF CRANE-FLIES (TIPULINAE) AS INDICATED BY CAPTURES IN A LIGHT TRAP AT ROTHAMSTED

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(*With Plate* 11 *and* 8 *Figures in the Text*)

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1. Introduction

Figures obtained by catching insects in a light trap at Rothamsted Experimental Station, Harpenden, form the basis of this study of the nocturnal activity of crane-flies of the sub-family Tipulinae (Diptera). The group was selected because of the economic importance of the larvae of a number of its species—notably *Tipula paludosa*, *T. oleracea* and *Pales flavescens*—and also because it was captured in numbers large enough to allow of statistical analysis of the influence of various climatic factors on its activity.

The light trap, its construction, situation and method of working have been described by Williams (1935). It was kept in use continuously (with occasional accidental stoppages), for four years—March 1933 to February 1937. The captures of Tipulinae during the first two years have been analysed by Pinchin & Anderson (1936). The present study is a continuation and extension of their work. A further two years' captures have been analysed and the results for the whole four years summarized.

It is important to remember that throughout this work the term "activity" is used in the sense of phototropic activity, i.e. the number of insects caught in response to light-trapping.

2. Numbers captured

(*a*) *Number of species*

During the first two years (1933 and 1934[1]), the total number of species of Tipulinae captured in the Rothamsted light trap was 11. In the succeeding two years (1935 and 1936) this number has been increased to 17, though none of the "new" species has been captured in anything but extremely small numbers. The common species, i.e. the first seven species occurring in Table 1, are still the same as in the first two years, viz.:

1. *Tipula paludosa* Meig.
2. *T. obsoleta* Meig.
3. *Pales maculata* Meig.
4. *P. flavescens* Linn.
5. *Tipula pagana* Meig.
6. *T. marmorata* Meig.
7. *T. oleracea* Linn.

Table 1

	1933		1934		1935		1936		1933–6	
Species	No.	% of total Tipulinae	No.	% of total Tipulinae	No.	% of total Tipulinae	No.	% of total Tipulinae	No.	% of total Tipulinae
T. paludosa	787	62·6	505	60·4	288	46·7	369	53·9	1949	57·4
T. obsoleta	159	12·6	138	16·5	89	14·4	102	14·9	488	14·4
P. maculata	129	10·3	87	10·4	19	3·1	24	3·5	259	7·6
P. flavescens	20	1·6	36	4·3	119	19·3	54	7·9	229	6·7
T. pagana	63	5·0	33	3·9	47	7·6	51	7·5	194	5·7
T. marmorata	43	3·4	22	2·6	17	2·8	45	6·6	127	3·7
T. oleracea	51	4·1	11	1·3	22	3·6	29	4·2	113	3·3
T. cava	—	—	—	—	7	1·1	4	0·6	11	0·3
T. luteipennis	4	0·3	—	—	—	—	—	—	4	0·1
T. fascipennis	—	—	2	0·2	2	0·3	—	—	4	0·1
T. vernalis	—	—	2	0·2	—	—	2	0·3	4	0·1
T. lunata	—	—	—	—	2	0·3	2	0·3	4	0·1
T. lateralis	—	—	—	—	3	0·5	1	0·1	4	0·1
T. variipennis	1	0·1	—	—	—	—	—	—	1	—
T. nigra	—	—	—	—	1	0·2	—	—	1	—
T. czizeki	—	—	—	—	1	0·2	—	—	1	—
T. peliostigma	—	—	—	—	—	—	1	0·1	1	—
All species	1257	—	836	—	617	—	684	—	3394	—
All species (excluding *T. paludosa*)	470	—	331	—	329	—	315	—	1445	—

Table 1, giving the yearly catches of each of the 17 species, has been arranged in order of total abundance of the separate species over the period of four years. Of the two genera represented, *Tipula* includes 15 species and the *Pales* only two. It is a curious fact that the greatest number of species in any one year—13—was recorded in 1935, the year of least abundance of individuals.

[1] For convenience the periods are referred to by the year in which the greater number of months falls, e.g. 1933 is really March 1933–February 1934, and so with the other three periods.

(*b*) *Numbers of each species*

The figure for the total catch per year is by no means constant, being very much larger in 1933 than in any of the succeeding three years (see Table 1). During the last two years, in fact, the combined total capture was only slightly greater than that of the first year alone. The differences between the yearly totals are very largely accounted for by fluctuation in the catch of *T. paludosa*, which was by far the most numerous species in any year. When the total catch was highest—1257 in 1933—the percentage of *T. paludosa* attained its greatest value of 62·6, and when the total catch was lowest—617 in 1935—the percentage of *T. paludosa* was reduced to 46·7, its smallest value. If the catches of *T. paludosa* are omitted, the numbers of all other species combined are seen to be very much more uniform. The figure is still rather higher for 1933, the year of greatest abundance, but practically constant in the following three years.

The ten rarer species never account for more than 2·6% of the total catch in any one year, and for the whole four years account for only 1% of the total.

3. Sex proportions

(*a*) *All Tipulinae*

Table 2, giving the proportions in which the sexes were captured, shows that in general the males of Tipulinae appear at light in greater numbers than the females. Although this holds true for the group as a whole it by no means holds for the individual species. In three of the "common" species

Table 2

	1933		1934		1935		1936		1933–6	
Species	Sex ratio ♂ : ♀	% ♂♂	Sex ratio ♂ : ♀	% ♂♂	Sex ratio ♂ : ♀	% ♂♂	Sex ratio ♂ : ♀	% ♂♂	Sex ratio ♂ : ♀	% ♂♂
T. paludosa	578 : 209	73·4	413 : 92	81·8	209 : 79	72·6	188 : 181	50·9	1388 : 561	71·2
T. obsoleta	33 : 126	20·8	29 : 109	21·0	24 : 65	27·0	50 : 52	49·0	136 : 352	27·9
P. maculata	124 : 5	96·1	86 : 1	98·9	15 : 4	78·9	22 : 2	91·7	247 : 12	95·4
P. flavescens	18 : 2	90·0	26 : 10	72·2	107 : 12	89·9	45 : 9	83·3	196 : 33	85·6
**T. pagana*	63 : 0	100·0	33 : 0	100·0	47 : 0	100·0	51 : 0	100·0	194 : 0	100·0
T. marmorata	4 : 39	9·3	2 : 20	9·1	1 : 16	5·9	9 : 36	20·0	16 : 111	12·6
T. oleracea	9 : 42	17·6	5 : 6	45·5	9 : 13	40·9	6 : 23	20·7	29 : 84	25·7
T. luteipennis	4 : 0	—	—	—	—	—	—	—	4 : 0	—
T. fascipennis	—	—	2 : 0	—	1 : 1	—	—	—	3 : 1	—
T. vernalis	—	—	2 : 0	—	—	—	1 : 1	—	3 : 1	—
T. variipennis	1 : 0	—	—	—	—	—	—	—	1 : 0	—
T. cava	—	—	—	—	0 : 7	—	1 : 3	—	1 : 10	—
T. lateralis	—	—	—	—	0 : 3	—	0 : 1	—	0 : 4	—
T. lunata	—	—	—	—	1 : 1	—	1 : 1	—	2 : 2	—
T. nigra	—	—	—	—	1 : 0	—	—	—	1 : 0	—
T. czizeki	—	—	—	—	0 : 1	—	—	—	0 : 1	—
T. peliostigma	—	—	—	—	—	—	1 : 0	—	1 : 0	—
All species	834 : 423	66·3	598 : 238	71·5	415 : 202	67·1	375 : 309	54·8	2222 : 1172	65·4
All species (excluding *T. paludosa*)	256 : 214	54·5	185 : 146	55·9	206 : 123	62·6	187 : 128	59·4	834 : 611	57·7

* Females are wingless.

Phot. 1.

Phot. 2.

Phot. 3.

Phots. 1—3. *Tipula paludosa*. 1. Male. 2. Female. 3. Part of catch from the light-trap.

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the males are more common at light than the females; in the other three the more "active" sex is the female. (In *T. pagana* only males are captured, since the females are wingless.)

The percentage of males in a year's catch varies between 71·5 (1934) and 54·8 (1936), mean 65·4. The fluctuations in this quantity are found, as in the total numbers of all species, to be largely caused by *T. paludosa*. If *T. paludosa* is omitted, the variability from year to year is very much reduced, the percentage of males then fluctuating between 62·6 and 54·5.

(*b*) *Separate species*

The species, other than *T. paludosa*, in which males are captured more abundantly than females are *Pales maculata*, *P. flavescens* and *Tipula pagana*. In the last-named species the female has only rudimentary wings and therefore cannot be captured in the trap. (As a matter of interest a single female specimen of *T. pagana* was captured in 1935. It is surmised that the insect either crawled into the trap or that it may possibly have been carried to the light by the male during the act of mating. This one specimen has not been included in any of the tables.) The three species in which females are in excess are *Tipula obsoleta*, *T. marmorata*, and *T. oleracea* with male percentages of 27·9, 12·6 and 25·7.

In the seven commonest species over the four-year period there are no values for the percentage of males between 27·9 and 71·2. In other words the sex which predominates, whether it be male or female, always accounts for more than two-thirds of the total catch. There is then in each species a marked tendency for one sex to predominate over the other.

4. Distribution

(*a*) *Monthly distribution*

(1) *All Tipulinae.*

Tipulinae spend the winter in the larval stage underground—as the well-known leatherjackets—and imagines were never captured in the light trap between the middle of November and the beginning of May. Every year the first appearance of a Tipulinid took place some time in May, the dates for the four years being respectively 6, 20, 5 and 22 May. In November, the last month of appearance of any species, the latest date of capture was the 16th in 1936. During the four years the total catch of all species for this latter month amounted to no more than nine specimens.

Instead of actual numbers, in many of the subsequent calculations logarithms have been used. By this means it has been found possible to arrive at a more accurate estimation of the relationships which exist between insect activity and the various climatic factors. On this system, if n be the actual numerical catch for a single night, or in some cases for a single period of one

night, the value of log $(n+1)$ is taken as a measure of the catch. Unity is added to the numerical value to avoid the use of "minus-infinity" (the logarithm of 0), when the catch is zero. When the logarithms have to be reconverted into numbers the anti-logarithm is taken and unity subtracted from it. The method of using logarithms instead of numbers has been explained by Williams (1935, 1937). Its great advantage lies in the fact that any

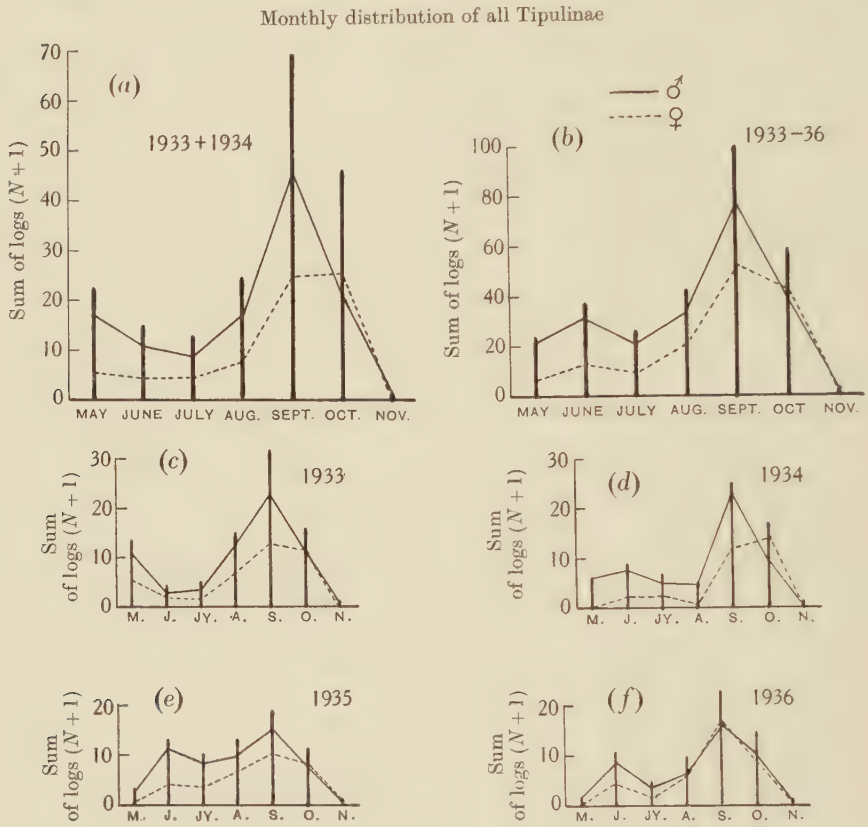

Fig. 1.

swamping effect introduced by a single very large catch is eliminated, and in every case in which they have been applied logarithms have been found to give more consistent results than numerical values.

A histogram of the monthly catches (using logarithms) by Pinchin & Anderson based on the first two years' figures showed a minor maximum in May and a major peak in September. (Reproduced in Fig. 1 (*a*).) The May peak was due to captures of *P. maculata*, and the latter to large numbers of *T. paludosa*. The addition to this diagram of the captures for a further two years has the effect of transferring the minor maximum from May to June, while the much greater September maximum is retained (Fig. 1 *b*). The change

in the month of the first maximum is due to the much greater abundance of *Pales flavescens* (chiefly active in June), in 1935 and 1936, and a great reduction in the catches of the May-flying *P. maculata*. A histogram has been drawn for each year (Fig. 1 *c–f*) and it is seen that only in 1933 was there a minor maximum in May. In all other years the diagram approximates more closely to the four-year diagram with the first peak in June. July is throughout a month of reduced frequency, the interval occurring between the maxima of activity of *P. flavescens* and *T. paludosa*.

Lines have been superimposed on the histograms to indicate the proportion of each sex in the monthly catches. As would be expected, with the general predominance of the male sex, the "male-line" approximates much more closely to the form of the histogram than does the "female-line". October is seen to be the only month in which, in general, females predominate over males. This is caused by the occurrence in October of the two species *T. marmorata* and *T. obsoleta* in which females are always captured in excess of males. There was a slight predominance of females over males observed in August and September of 1936 which was due to an increase in the proportion of females of *T. paludosa* in that year.

(2) *Separate species.*

The dates of capture of the seven common species in each of the four years are set out in Fig. 2. With the two exceptions of *T. oleracea*, which appears in all seven months from May to November, and *T. paludosa*, with a somewhat shorter range, each species has a comparatively well-defined period of activity as an imago. Particularly noticeable in this respect are the three autumn species, *T. marmorata*, *T. obsoleta* and *T. pagana*.

Tipula oleracea first appears in May or early June. It continues to be captured in small numbers for the succeeding five or six months. In each year there is evidence that the species is two-brooded, the interval between broods occurring in either July or August. In Fig. 3*a* an attempt has been made, by combining the captures for the four separate years, to determine the periods of greatest activity for the species. The days of the months of activity have been set out horizontally and the length of each vertical column represents the four-year sum of the numerical captures of *T. oleracea* for the corresponding date. By superimposing a seven-day running mean on the diagram, it can be seen that there is evidence in favour of double-broodedness in *T. oleracea*. The first brood seems to attain a period of greatest activity between the middle of May and the end of June—the second between mid-August and the end of September. In each case the appearance of a brood seems to be, on an average, comparatively evenly distributed over a period of one and a half months.

Pales maculata is usually the first species to be captured in any one year. The mean date for *P. maculata* is 14 May and for *T. oleracea* 20 May. Unlike *T. oleracea*, *P. maculata* has a comparatively short and very much more clearly defined period of activity. With the exception of a single specimen caught on 22 July 1935 (Fig. 2) the period of activity of this species was confined to May and June, the mean date of last appearance being 27 June. Fig. 3*b* shows a rapid rise to a maximum in the second half of May, followed by a gradual falling off until the end of June.

Dates of occurrence of common Tipulinae in light-trap
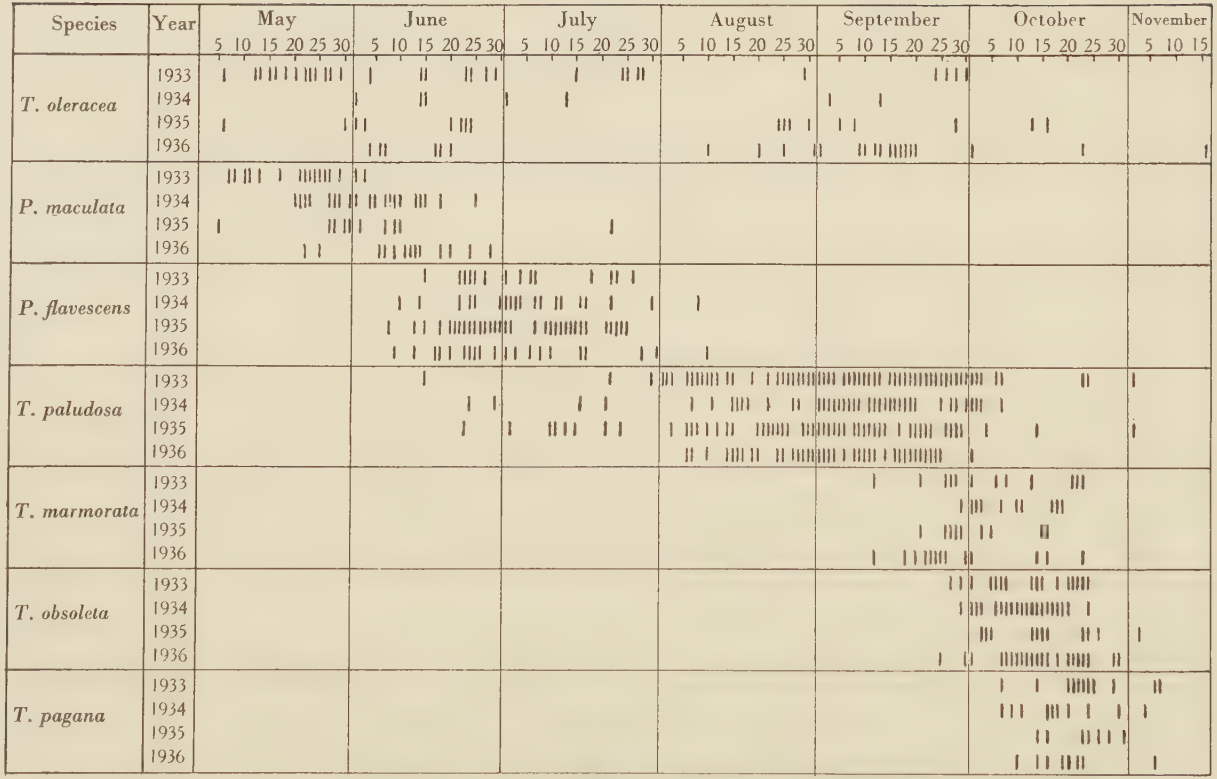
Fig. 2.

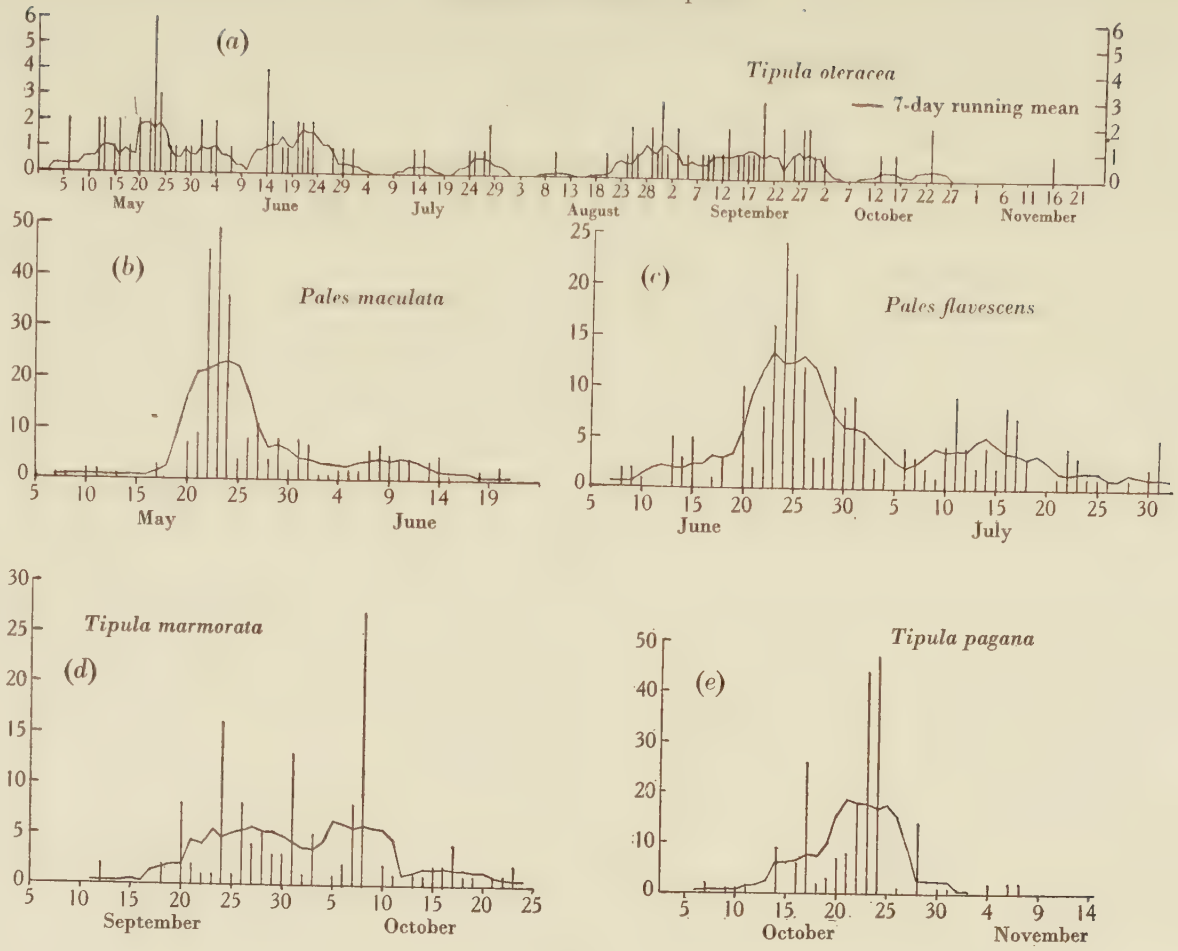
(a)
Tipula oleracea
7-day running mean
May
June
July
August
September
October
November
(b)
Pales maculata
May
June
(c)
Pales flavescens
June
July
(d)
Tipula marmorata
September
October
(e)
Tipula pagana
October
November

Fig. 3.

Pales flavescens is another species whose imaginal activity seems to be confined to a period of almost exactly two months. In this case the months are June and July, the mean dates of first and last appearance—11 June and 2 August—being about one month later than the corresponding dates for *P. maculata*. In distribution of activity *P. flavescens* is again very similar to the preceding species: a rapid increase in the catch in the middle of June, a maximum towards the end of the month, but a much more gradual decrease until the end of the following month—in this case July. The maximum for *P. flavescens* is not quite so sharply defined as for *P. maculata*, and the decrease is more gradual (see Fig. 3*c*).

With **Tipula paludosa** the period of activity is again comparatively long. Between the mean date of first (2 July) and last (19 October) appearances the species is active for about three and a half months. It is possible that this length is due to there being two broods of *T. paludosa* in the year. But there is little, if any, evidence in support of this view to be gained from the dates of capture of the species. No distinct break, such as is evident in the case of *T. oleracea*, can be distinguished at any particular time in the period of activity (see Fig. 2). While the distribution does not afford any positive evidence of a double brood, it does not preclude the possibility that there are two broods of *T. paludosa* in the year.

Although specimens of *T. paludosa* are captured in June and July (possibly representatives of a small first brood), the main frequency of the species is confined to August and September, when it reaches great abundance, being about four times as numerous as the next most common species. Of the four-year total of 1949, only 101 specimens were taken in other months. 16 of the latter occurred in June and July, and 85 in October and November (including a catch of 44 on 1 October 1933).

Since *T. paludosa* and *T. obsoleta* were the two most numerous species, their annual distributions have been set out in Fig. 4 in addition to their four-year distributions, to show the extent to which the periods of greatest activity of a species vary from year to year.

For *T. paludosa* the smoothed four-year diagram shows a peak not far removed from 14 September. The increase takes place gradually from the middle of August; the decrease appears to be more rapid and there is little activity after the first week in October.

Tipula marmorata, the first of the three single-brooded autumn species, had an average period of activity of 32 days between mean dates 18 September and 20 October. The maximum seems to occur somewhere between 24 September and 10 October, during which period there was no very pronounced peak during the four years under consideration (Fig. 3*d*).

Tipula obsoleta with an average length of brood of exactly one month—28 September to 28 October—attained greatest abundance some 16 or 17 days later than *T. marmorata*. The peak in *T. obsoleta* is slightly more marked than in the latter species, and appears to be somewhere between 15 and 22 October (Fig. 4).

Tipula pagana, the last of the common species, besides being notable for the rudimentary wings of the female, appears also to be remarkable for the shortness of its period of activity. Between mean dates 9 October and 4 November the average period of capture was 26 days. It never appeared before 7 October or later than 7 November. A well-defined maximum, clearly indicated by the seven-day running mean preceded by a rapid rise and succeeded by a rapid fall, occurred within one or two days of 21 October (Fig. 2).

(3) *Separate sexes.*

In an attempt to discover whether there is any difference in the seasonal occurrence of the separate sexes the two species *T. paludosa* and *T. obsoleta* were selected. In addition to being the two most numerous, these species happen to be the only two which provided sufficient numbers of both sexes for this purpose.

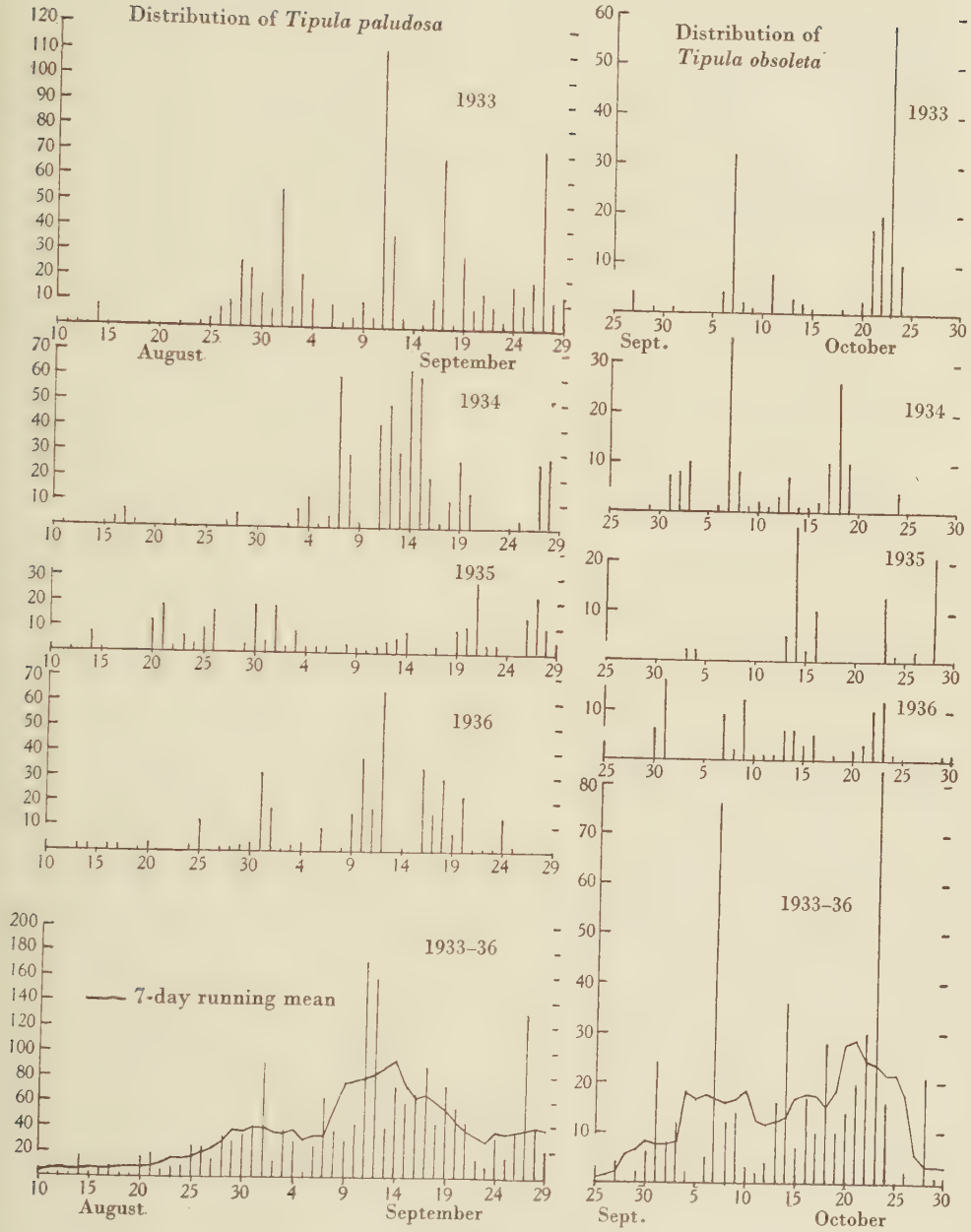
Distribution of *Tipula paludosa*
1933
1934
1935
1936
1933–36
7-day running mean
August
September
Distribution of
Tipula obsoleta
Sept.
October

Fig. 4.

Fig. 5 shows a seven-day running mean of the captures of each sex in each of these two species.

The graphs for *T. paludosa* indicate a close similarity in the periods of activity of the two sexes. It also shows that when the species is most active, i.e. in the middle of September, the proportion of males is at its highest. On either side of the maximum, i.e. at either end of the month, the proportions of the sexes are much more nearly equal. Whereas the peak for the males is very definitely marked, the activity of the females seems to remain at a comparatively constant level between dates around 29 August and of 19 September.

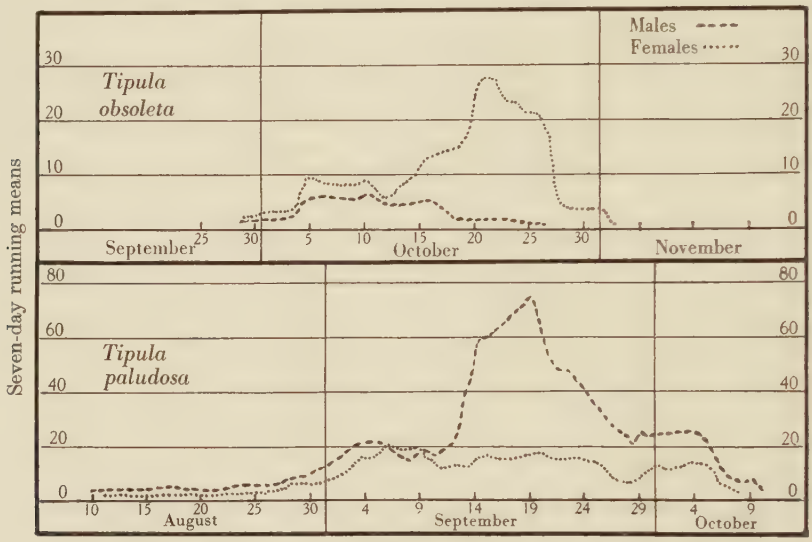

Fig. 5.

With *T. obsoleta* the story is very different. Here it is found that one sex definitely precedes the other in time of maximum activity. In this species females are captured in much greater abundance than males, and the activity of the former does not reach a maximum until some 11 days after that of the latter. The dates of maximum are about 21 October for females and 10 October for males. Both sexes make their first appearance in the trap at about the same time, but the activity of the male has decreased almost to zero before the female reaches its peak.

(*b*) *Distribution throughout the night*

(1) *All Tipulinae.*

By means of a series of eight killing-bottles and a clockwork bottle-changing mechanism, the light trap divided up the catch of insects for each night into eight successive equal portions. The night is considered to start half an hour after sunset and end half an hour before sunrise. It is therefore

possible, by studying the catches in successive periods, to investigate the distribution of activity of any species throughout the night.

For the Tipulinae as a whole the distribution of activity during the night is illustrated by Fig. 6. The maximum of activity is observed in the period immediately after sunset, the following period showing a slight reduction. During periods 3 and 4 there is a rapid fall in activity until midnight. For the second half of the night—from midnight to dawn—the activity is maintained at a fairly steady minimum level with a slight increase towards sunrise.

The separate sexes display considerable differences in behaviour. Except that the activity of the males appears to be equally distributed over the first

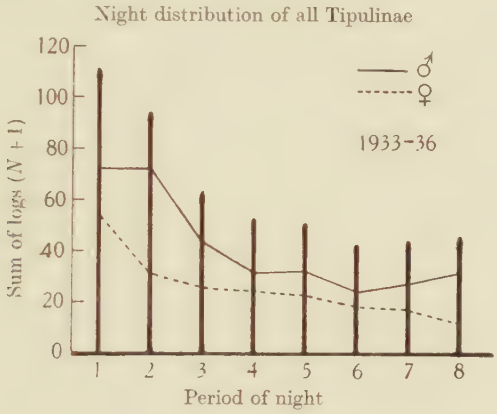

Fig. 6.

two periods their distribution follows very closely the distribution for the two sexes combined. The females, on the other hand, show a very marked peak of activity in the first period, after which an almost continuous very gradual decrease take place throughout the remaining hours of the night.

(2) *Separate species.*

Taking the individual species in turn:

Pales maculata (Fig. 7*a*) shows a very evident maximum of abundance immediately after sunset with a continuous and rapid fall until midnight. Thereafter a more or less constant low level of abundance is maintained until dawn. The very small numbers of females captured were confined almost entirely to the first half of the night.

T. oleracea (Fig. 7*b*) shows no marked period of maximum activity. Probably the total numbers captured were not large enough to establish any definite distribution. The females maintain a steady distribution throughout all but the first and last periods, at which times it is slightly less active. There is possibly a peak of activity for this sex at midnight. Males were most active just after sunset.

Pales flavescens (Fig. 6*c*), displays greatest activity in the two periods midway between sunset and midnight. There follows a sudden fall after period 3 and irregular distribution from then until dawn, with evidence of a minimum half-way between midnight and sunrise. Females in this species again account for but a small percentage (6·7) of the total, and

display no definite peak of activity. A peak, if it does exist, probably coincides with that of the males.

T. paludosa (Fig. 8) very closely resembles the total Tipulinae. A decidedly large proportion of this species is captured in the first two periods of the night. Thereafter is a sudden fall in activity until just before midnight, a more gradual fall during the next three periods and a definite increase as dawn approaches. For males the maximum is attained in the period commencing about $1\frac{1}{2}$ hr. after, instead of immediately after, sunset and the rest of

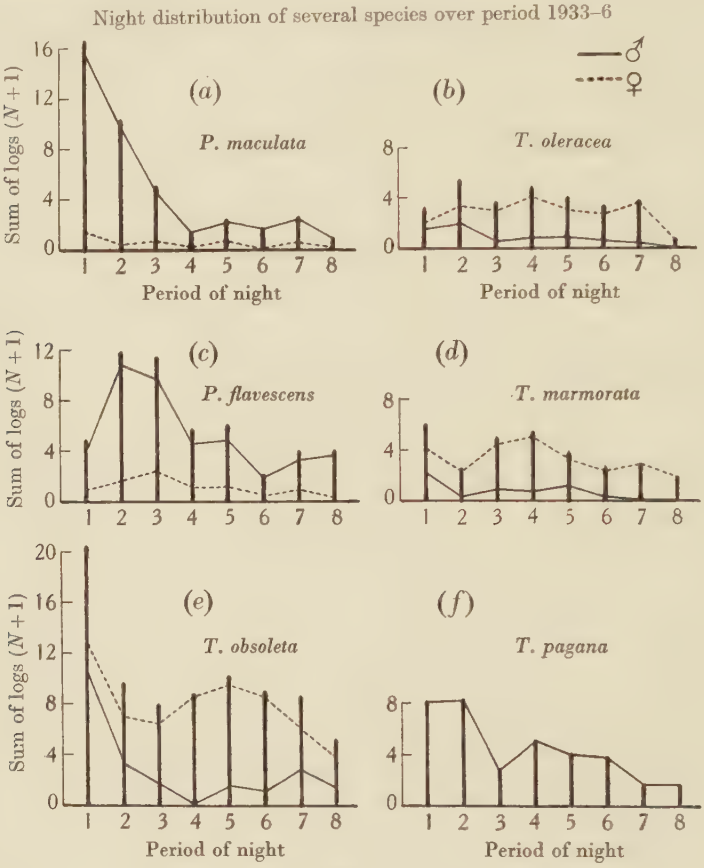

Fig. 7.

the distribution is closely similar to that of the species as a whole. The females attain a very definite maximum slightly earlier than the males, followed by a very sudden fall in period 2 and a further gradual decrease until sunrise.

T. marmorata (Fig. 7*d*) like *T. oleracea*, shows a comparatively uniform night activity. There is a definite maximum immediately after sunset, a slight fall in activity in the succeeding period, a secondary maximum at midnight and a further continuous fall until dawn. From diagrams for the four separate years it is found that the evidence for one maximum immediately after sunset and for another in the region of midnight is quite definite in every case. This applies to the females as well as to the species as a whole. The distribution of the small number of males is similar, with the secondary maximum slightly later than for the females.

T. obsoleta (Fig. 7 *e*) is very similar to *T. marmorata*. By comparison *T. obsoleta* shows an even more definite maximum just after sunset, while the secondary maximum occurs somewhat later—about an hour after midnight. The females again being greatly in the majority, have a similar distribution to the species as a whole. But the males differ notably in that the maximum activity in period 1 is followed by a minimum at or about midnight and a secondary

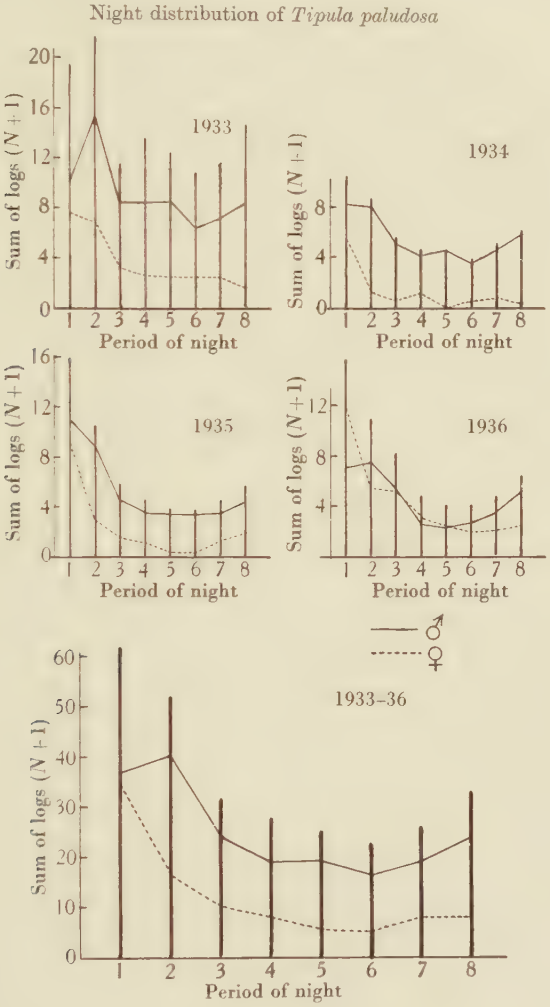

Fig. 8.

maximum in period 7. Here again yearly diagrams bring out the consistency of the two maxima, one at sunset and another which varies in "period" from 5 to 7. In general this secondary maximum occurs shortly after midnight.

T. pagana (Fig. 7 *f*), shows on the whole no very marked preference for any particular period of the night. In the usual way the first part of the night sees its greatest abundance but after period 2 the distribution is devoid of any well-marked feature. There is some evidence of a secondary maximum round about midnight.

For all Tipulinae, then, the peak of night activity is unquestionably attained in the early periods of the night—almost immediately after sunset. Taken as a whole there is then a gradual decrease in activity—interrupted by a slight secondary maximum just after midnight—throughout the rest of the night. The peak activity of the males is more evenly distributed over periods 1 and 2 than for the females, whose greatest abundance is quite definitely confined to period 1. This difference has been interpreted by Pinchin & Anderson as an "earlier flight of females". It seems more likely that both sexes attain maximum activity at much the same time, and that the males remain active for rather longer than do the females.

Taking the separate species, without exception greatest abundance is realized in one of the first two periods—in the majority of cases in the former of the two. Moreover a secondary maximum of activity is almost invariably attained later in the night—usually just after midnight. The only notable exception is *T. paludosa*, in which alone is observed a complete absence of any peak near midnight, coupled with a marked secondary maximum just before dawn. The "dawn maximum" of activity observed in the diagram for all Tipulinae is therefore entirely attributable to this one species, and in fact to the male sex of the species.

5. Influence of temperature on nocturnal activity

On the figures for two years Pinchin & Anderson were able to conduct a preliminary analysis of the effect of maximum and minimum temperatures on the captures of Tipulinae. A further two years' figures, in addition to verifying their conclusions, makes it possible to investigate the influence of temperature in much greater detail. By reason of its invariable abundance throughout the month of September, *T. paludosa* lends itself particularly to a detailed analysis of temperature effects. Consequently most of the following results are based on this species and this one month. Evidence has been obtained, however, by studying the effects of temperature on *T. paludosa* in August (when it is much less abundant than in September), and on *T. obsoleta* in the month of October, which definitely indicates that conclusions based on the captures of *T. paludosa* in its most active month can be applied to the sub-family as a whole. The further fact that in *T. paludosa* the predominant sex is the male whereas the female is the more active sex in *T. obsoleta* supports the above contention. No other single species was captured in numbers large enough to allow of similar statistical treatment.

(*a*) *Minimum and maximum temperature*

To study the influence of minimum temperature on the captures of *T. paludosa* two series of values were correlated (Table 3):

(1) Departures of the log catch of the species from a 15-day running mean.

(2) Departures of minimum temperature from a similar mean.

Table 3

Species	Month	Correlation	Partial correlation	Regression	Partial regression
Relation with minimum temperature					
1933					
T. paludosa	**Sept.**	**0·77**	**0·75**	**0·082**	**0·087**
,,	Aug.	0·48	0·35	0·043	0·035
T. obsoleta	Oct.	0·76	0·57	0·059	0·054
1934					
T. paludosa	**Sept.**	**0·77**	**0·67**	**0·076**	**0·066**
,,	Aug.	0·55	0·19	0·034	0·012
T. obsoleta	Oct.	0·23	0·35	0·016	0·026
1935					
T. paludosa	**Sept.**	**0·62**	**0·24**	**0·055**	**0·022**
,,	Aug.	0·52	0·40	0·045	0·039
T. obsoleta	Oct.	0·41	0·26	0·027	0·024
1936					
T. paludosa	**Sept.**	**0·71**	**0·70**	**0·098**	**0·103**
,,	Aug.	0·57	0·48	0·049	0·049
T. obsoleta	Oct.	0·57	0·64	0·056	0·070
1933–6					
T. paludosa	**Sept.**	**0·72**	**0·64**	**0·075**	**0·071**
,,	Aug.	0·52	0·42	0·042	0·033
T. obsoleta	Oct.	0·50	0·48	0·037	0·046
Relation with maximum temperature					
1933					
T. paludosa	**Sept.**	**0·25**	**−0·15**	**0·030**	**−0·013**
,,	Aug.	0·37	0·13	0·023	0·009
T. obsoleta	Oct.	0·62	0·08	0·081	0·011
1934					
T. paludosa	**Sept.**	**0·56**	**0·21**	**0·063**	**0·019**
,,	Aug.	0·63	0·41	0·043	0·033
T. obsoleta	Oct.	−0·10	−0·17	−0·008	−0·022
1935					
T. paludosa	**Sept.**	**0·78**	**0·64**	**0·094**	**0·075**
,,	Aug.	0·38	0·12	0·025	0·008
T. obsoleta	Oct.	0·33	0·04	0·037	0·006
1936					
T. paludosa	**Sept.**	**0·20**	**−0·12**	**0·031**	**−0·014**
,,	Aug.	0·05	−0·12	0·003	−0·001
T. obsoleta	Oct.	−0·03	−0·37	−0·014	−0·040
1933–6					
T. paludosa	**Sept.**	**0·43**	**0·094**	**0·054**	**0·010**
,,	Aug.	0·35	0·11	0·023	0·014
T. obsoleta	Oct.	0·21	−0·16	0·023	−0·019

In every year the value of the correlation coefficient was found to be positive and significant, varying between 0·77 in 1933 and 0·62 in 1935 (Table 3, heavy type). A similar correlation for each year with maximum temperature gave values which in two years were significant and in two years were not. The correlation for the four years combined was just significant at the 2% level. It is evident therefore that whereas minimum temperature invariably plays a significant part in determining the size of catch of *T. paludosa*, the effect of maximum temperature is not nearly so important. These facts are brought out more clearly when partial correlation coefficients are considered. When the influence of maximum temperature has been eliminated, the partial correlation with minimum temperature (0·64) is only slightly less

than the "total" correlation value (0·72), and is still on the four years' working well above the 2% level of positive significance. The partial correlation with maximum temperature, on the other hand, is negative in two years out of four and far from being significant (0·094) over the whole period.

Only in 1935 is the partial correlation with minimum temperature non-significant. This year too is the only one in which the partial correlation with maximum temperature is significant. In 1935 the mean minimum temperature for September was considerably lower than in the other three years, 48·9 as compared with 51·5, 50·2 and 51·7. It therefore seems probable that the influence of maximum temperature is only appreciable when minimum temperature is low. In support of this conclusion it is observed that the correlation with maximum temperature is approximately inversely proportional to the value of the mean minimum temperature. A correlation between the two series of values gives a figure of −0·9987 which is significant at the 1% level.

A consideration of regression coefficients again illustrates the overwhelming influence of minimum temperature. The four-year regression and partial regression on minimum temperature are respectively 0·075 and 0·071, as compared with 0·054 and 0·010, the corresponding figures for maximum temperature. The reduction in value, by taking a partial regression, is again slight in the first instance and large in the second. The regression and partial regression on minimum temperature mean that an increase in the log catch of 0·30 (equivalent to a doubling of the numerical catch) is brought about on an average by a rise of 4–4½° F. in minimum temperature. Whereas, on a partial regression of 0·010, the increase in maximum temperature required to double the catch would be more than 30° F. As this latter partial regression is not significant and is made up of two negative and two positive values it is not possible to determine how much more important is minimum than maximum temperature.

Correlations with minimum and maximum temperatures, using actual numbers instead of logarithms, give very similar results (Table 4). The figures show a slight general reduction on the former values, but for the four years the partial correlation with minimum temperature is always significant,

Table 4. *Numerical catches of* Tipula paludosa *in September*

T. paludosa	September	Correlation	Partial correlation	Regression
Related to minimum temperature	1933	0·68	0·60	3·62
	1934	0·66	0·48	1·87
	1935	0·64	0·42	0·80
	1936	0·57	0·59	2·04
	1933–6	0·59	0·53	2·03
Related to maximum temperature	1933	0·18	−0·29	1·10
	1934	0·59	0·34	1·92
	1935	0·58	0·29	1·08
	1936	0·08	−0·20	0·33
	1933–6	0·30	−0·004	1·26

that with maximum temperature is never significant and on an average the latter is negative. One interesting difference observed when numbers are used is that neither correlation nor partial correlation with maximum temperature is ever greater than the corresponding figure with minimum temperature. In this respect numbers give a slightly greater consistency than logarithms, but when regressions on the two systems are calculated the advantage of using logarithms becomes markedly apparent. For example, the numerical regression on minimum temperature varies between 0·80 and 3·62, depending very largely on the total abundance of the species in the year concerned. The variability of the corresponding regressions on the logarithm basis is, in comparison, very small—extreme values being 0·055 and 0·098—and is independent of numerical abundance. These figures indicate quite clearly that, as would be expected, the catch of *T. paludosa* increases with temperature in a geometric rather than in an arithmetic ratio. Herein, then, lies a very strong argument for the use of the logarithmic system.

Statistical analysis of the relation between catches of *T. paludosa* in August and of *T. obsoleta* in October, and maximum and minimum temperature, affords striking corroboration of the above conclusions. For *T. paludosa* (Table 3) the correlation with minimum temperature is again always positive and always significant. The values, however, are not quite so high as they are in September, due to a larger number of zero captures which always reduce the correlation. Likewise the regression, again noticeably consistent, shows that in August when the species has not attained maximum activity, the increase in minimum temperature required to double the catch is in the neighbourhood of 7° F.—considerably higher than in September. For *T. obsoleta* (Table 3) the relationships are substantially similar. Once more the correlation and partial correlation with minimum temperature are positive and in general significant. With maximum temperature they are again non-significant, the partial correlation being negative. The partial regression on minimum temperature, value 0·046, indicates a similar average increase of about 7° F. as being necessary to double the catch of *T. obsoleta*.

(*b*) *Daily range of temperature*

A study of the relation between catch of *T. paludosa* and difference between maximum and minimum temperature (daily range), indicates a further significant relationship. For these calculations departures from 15-day running means were again used, since there is a progressive shortening of the daily temperature range throughout the month of September. The values of correlations and regressions were found invariably to be negative, and significant in three years out of four. For the four years combined a correlation coefficient of $-0{\cdot}45$ is definitely significant. It appears therefore that a small daily range in temperature is favourable to a large capture of this species. This conclusion is confirmed by the often observed fact that on a clear night—when there is

always a rapid fall in temperature—the conditions are unfavourable for insect activity. The four-year regression figure of −0·052 indicates that a reduction of about 6° F. in the daily range of temperature will effect a doubling of the catch of *T. paludosa* in its month of greatest activity (Table 5).

Table 5. Tipula paludosa *and difference between maximum and minimum temperatures* (*daily range*)

September	Correlation	Regression
1933	−0·54	−0·058
1934	−0·36	−0·041
1935	−0·16	−0·019
1936	−0·68	−0·094
1933–6	−0·45	−0·052

Catch is doubled by a reduction of approximately 6° F. in daily range.

This significant relationship with daily temperature range may actually be deduced from the nature of the relationships with maximum and minimum temperature. From the facts of a significant correlation with minimum temperatures and a non-significant relationship with maximum temperature it follows that there will be a significant correlation with the difference between the two. The value of the latter correlation coefficient can, however, only be determined by relating directly the two series of values—insect catch and temperature range. Remembering that no corrections have been made for any other factors which are known to affect activity, e.g. wind, cloud, moonlight, it still seems evident that temperature plays a very important part in determining variations in the catch of Tipulinae (as exemplified by *T. paludosa* and *T. obsoleta*) within a single year. Correlations between all Tipulinae and minimum temperature throughout the six summer months gave coefficients of 0·46 and 0·55 respectively in 1935 and 1936. Since each of these figures is based on about 170 observations their significance is high.

Minimum temperature is then unquestionably the more important single thermal factor in determining activity in Tipulinae. By comparison, maximum temperature has relatively little effect on the abundance of the group. Only when the minimum temperature is low, and its influence reduced, does the effect of maximum temperature become apparent. Additional evidence for this last conclusion is found in the observation that the correlation with maximum temperature is very roughly inversely proportional to that with minimum temperature.

The activity of Tipulinae is therefore: (1) very definitely favoured by a high minimum temperature, (2) definitely favoured by a small difference between maximum and minimum temperature, (3) little affected by changes in maximum temperature at least in so far as these are independent of minimum temperature.

6. Influence of cloud and moonlight on activity

In dealing with the influence of cloud and moonlight on the captures of all Tipulinae, the system devised by Dr C. B. Williams (1936) has been adopted. This system differentiates nine different combinations of conditions of cloudiness and moonlight. The nights of the six summer lunar months are divided into: (1) nights in the full-moon weeks; nights in the no-moon weeks; and nights in intermediate weeks; (2) nights of less than 10% cloud; 10–90% cloud; and more than 90% cloud. The nine possible combinations of the above two series are then set out in a square diagram as illustrated in Table 6.

Table 6. *All Tipulinae. Percentage of mean catch*

		Clear	Intermediate	Cloudy	
Full moon	1933	53	49	150	63
	1934	15	129	107	59
	1935	39	78	87	70
	1936	10	60	128	54
	1933–6	**31**	**69**	**111**	**63**
Intermediate	1933	66	72	274	107
	1934	68	162	68	111
	1935	68	118	109	97
	1936	46	85	190	106
	1933–6	**63**	**104**	**160**	**103**
No moon	1933	54	183	234	133
	1934	88	184	231	161
	1935	57	141	341	156
	1936	49	135	281	134
	1933–6	**60**	**163**	**265**	**142**
	1933	59	87	239	
	1934	51	152	114	
	1935	59	109	154	
	1936	36	88	186	
	1933–6	**53**	**106**	**166**	

These figures have been calculated in a series of steps. In the first place the actual log catch of all Tipulinae for each night in the six summer lunar months is placed in the appropriate square of the diagram, according to the prevailing conditions of moonlight and cloud. The mean log catch for each category is then calculated. These mean log catches are reconverted into numbers by taking the antilogarithm in each case and subtracting unity. And finally each of these numbers is expressed as a percentage of the mean catch for the whole period concerned, whether it be one summer or four summers combined, calculated in the same way by reconversion of the appropriate mean logarithm.

The minimum catch, approximately one-third of the mean, is recorded on clear nights of the full-moon weeks, whereas the maximum catch of more than two and a half times the mean occurs in cloudy nights in the weeks of no moon. Expressing this result in another way, the activity of Tipulinae under the most favourable conditions of cloud and moonlight is some eight or nine times as great as that attained in the least favourable circumstances. Between these two extremes there is a consistent rise in catch from full-moon periods to no-moon periods and from clear nights to cloudy nights.

On the right-hand side and bottom of the table are figures summarizing respectively the influence of moonlight irrespective of cloud, and the influence of cloud independent of moon. Between nights of full moon and nights of no moon the difference in percentage of mean catch is 79: between clear nights and cloudy nights it is 113. It therefore appears that both cloudiness and moonlight have marked effects on the captures of Tipulinae, but that the influence of cloud is about one and a half times as great as that of moonlight.

In the preceding table no account has been taken of fluctuations in minimum temperature. Table 7 shows that the minimum temperature varies considerably with prevailing conditions of cloud, but is unaffected by varying phases of the moon. On an average for the four years the minimum temperature was 1·88° below the normal on clear nights and 2·18° above normal on cloudy nights. The mean minimum temperature on a clear night was therefore almost exactly 4° F. below that of a cloudy night. In view of the importance of minimum temperature in determining activity of Tipulinae it seemed likely that this temperature difference must largely, if not entirely account for the observed difference between catches on clear and cloudy nights. Accordingly the figures were adjusted statistically to exclude the influence of minimum temperature. When all pure temperature effect had been eliminated the resulting difference between clear and cloudy night captures was found to be positive but non-significant. Though there remained some evidence of an independent cloud effect, in that catches over the four-year period were still slightly lower on clear than on cloudy nights, it appears that on the whole the observed influence of cloud conditions on the activity of Tipulinae may be almost entirely attributed to related variation in minimum temperature.

Table 7. *Minimum temperature. Four-year summary of mean departures from monthly running means*

	Clear	Intermediate	Cloud	
Full moon	−1·50	−0·63	+1·88	−0·27
Intermediate	−2·06	−0·10	+2·14	−0·05
No moon	−1·93	+0·08	+2·52	+0·15
	−1·88	−0·18	+2·18	

For the four years involved the temperature on a night of no moon was on an average 0·42° F. higher than on a night of full moon. This result can only be regarded as accidental, since there is obviously no relation between minimum temperature and the phase of the moon. The accidental nature of the final figure is borne out by observation of the separate yearly figures. The warmest nights in the four years are quite independently arranged in the various categories of moonlight, falling once in the full-moon period, once in the intermediate, and twice in the no-moon period.

The effects of moonlight and cloud on the activity of Tipulinae are therefore: (1) Both factors have a marked influence. (2) Optimum conditions are complete cloudiness and no moon. (3) Least favourable conditions are complete

absence of cloud and a full moon. (4) Between these extremes there is a consistent increase in catch with decrease of moonlight and increase of cloud. (5) The catch under optimum conditions is some eight or nine times as great as when conditions are least favourable. (6) The effect of cloud, almost all of which may be attributed to the related minimum temperature, is to treble the catch of a clear night. (7) The catch on a night of no moon is rather more than twice that on a moonlight night.

7. Summary

1. The total number of crane-flies of the sub-family Tipulinae captured in a light trap at Rothamsted Experimental Station in the four years 1933–6 was 3394. This number comprises seventeen species, seven of which were comparatively numerous in each of the four years. By far the most common single species is *Tipula paludosa*, accounting for 57·4% of the total capture. The ten "rare" species accounted for no more than 1% of the total.

2. *Sex proportions* show that in general males are attracted to light in larger numbers than are females: the former comprise 65·4% of the total catch. Species in which males predominate are *Tipula paludosa*, *Pales flavescens*, *P. maculata* and *Tipula pagana*. (In the last-named species the females are wingless.) Species in which females predominate are *Tipula marmorata*, *T. obsoleta* and *T. oleracea*.

3. *Monthly distribution.* Greatest activity for the group as a whole is recorded in September and is due to *T. paludosa*. A minor peak occurs in June as a result of the activity of *P. flavescens*. July is throughout a month of reduced activity. It is probable that *T. oleracea* alone is definitely double-brooded, and that *T. paludosa* may also have two broods in the year; but the other five species are clearly single-brooded.

Species	Mean period of activity	Length of period days	Time of maximum activity
T. oleracea	20 May – 4 Oct.	137	Brood I, mid-May to end of June Brood II, mid-Aug. to end of Sept.
P. maculata	13 May –27 June	45	Latter half of May
P. flavescens	11 June– 2 Aug.	52	Latter half of June
T. paludosa	2 July –19 Oct.	109	Middle of Sept.
T. marmorata	18 Sept.–20 Oct.	32	End of Sept.
T. obsoleta	28 Sept.–28 Oct.	30	Middle of Oct.
T. pagana	9 Oct. – 4 Nov.	26	About 21 Oct.

4. *Night distribution.* Activity of Tipulinae is invariably greatest just after sunset, and is maintained at a maximum slightly longer in males than in females. A gradual decrease in activity after the sunset maximum is interrupted by a slight secondary maximum near midnight and then continues until sunrise. The only exception to this generalization is *T. paludosa* which shows no maximum at midnight and a definite rise in activity towards dawn. The activity of males follows the general trend for the group more closely than that of females. For the separate species examined the primary maximum

invariably occurs in the first quarter of the night, and there is almost invariably a secondary maximum, usually just after midnight.

5. *Influence of temperature* was investigated by means of correlations and regressions, both total and partial, with maximum and minimum temperature. The influence of daily range in temperature was also examined. From this study the following conclusions emerge: (1) activity is very definitely favoured by a high minimum temperature; (2) activity is definitely favoured by a small difference between maximum and minimum temperatures—daily range; (3) activity is little affected by changes in maximum temperature, at least in so far as these are independent of minimum temperature.

At the time of greatest activity of the group it appears that a rise of 4–4½° F. in the minimum temperature will effect a doubling of the catch. The same result is produced by a reduction in the daily range of temperature of some 6° F.

6. *Influence of cloud and moonlight.* Both factors have a marked effect on the captures of Tipulinae. Optimum conditions are absence of moonlight and complete cloudiness. The converse conditions of full moon and no cloud are the least favourable to activity. Between these extremes there is a consistent increase in catch with increasing absence of moon and presence of cloud. The catch under optimum conditions is eight or nine times as large as in the least favourable circumstances. On a night of no moon the insects are rather more than twice as numerous as on a night of full moon. The effect of cloud, almost all of which may be attributed to the related minimum temperature is to treble the catch of a clear night.

8. Acknowledgements

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A POPULATION STUDY OF SUBTERRANEAN SOIL COLLEMBOLA

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(*With 5 Figures in the Text*)

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1. Introduction

It is well known that large numbers of different species of animals are found in the soil. At Rothamsted, Baweja (1939), found 275 different species in the soil fauna, while Frenzel (1936) found a total of 422 in various parts of Germany. In the present study no attempt was made to identify all the forms found. Attention has been concentrated on that part of the fauna which is truly subterranean. The majority of the animals commonly designated "soil" belong in fact to the surface or sub-surface. Though they may be found at considerable depths in arable land, in the more stable environment of the meadow they keep to the top. They are active animals, with body pigment and eyes, and they live in that ill-defined region where stem merges into root, where the plant covering protects delicate forms from climatic extremes, but daylight penetrates and there is more vegetation present than actual soil.

Below this there is a region of perpetual darkness, inhabited by a community of sluggish white blind animals whose modifications recall those of the cave fauna. Some are in fact recorded as cave forms (*Onychiurus armatus*, *O. ambulans*, *Tullbergia krausbaueri*). In the area under consideration this "truly subterranean" fauna consists of Symphyla, four species of Onychiuridae, and occasional specimens of the Achorutid *Anurida granaria*.

Pauropods and Protura are also found sometimes. Chilopods, the larvae of Elateridae and other beetles, larvae of Tipulidae and other flies, and earthworms, are also encountered deep in the soil. These animals, however, are of a different order of size from the Onychiuridae, and apart from the earthworms, are normally concentrated near the surface.

The relationship between the large animals and the Onychiuridae is obscure. It has been conjectured that Collembola and mites perform in the economy of the soil a role analogous to that of the animal micro-plankton of the soil—themselves herbivorous, being preyed on by larger carnivores. But this attractive proposition lacks concrete demonstration, and it is not impossible that the larger animals are in fact quite independent of the smaller. The present investigation can contribute nothing in this direction, for the study of, for examples, wireworms, has been shown by Jones (1937) to require samples as large as 1 sq. ft., which is impossibly big for Collembola investigations.

The present study is concerned with the Onychiuridae, of which four species were present—*Onychiurus armatus* Tullb., *O. ambulans* Nic., *Tullbergia quadrispina* Börner and *T. krausbaueri* Börner. These are all shining white naked animals, with short legs and no springing apparatus. The antennae, though short, are very sensitive and quiver continuously while the animals are walking. Digging is impossible for these soft feeble beasts, and they move only through the pores of the soil. Ford (1935) has shown that they are exterminated when the soil is made non-porous. *O. armatus* is a cosmopolitan species. Handschin gives for its habitats: under stones, in earth, and under bark. Frenzel regards it as a permanent inhabitant of meadow soil and a "Leitform" (one tolerating a wide range of habitats). In the United States it is a minor pest of sugar-cane (Spencer & Stracener, 1930; Ingram, 1931). Strebel (1932) found it very sensitive to sudden strong light, but as Cameron (1917) noticed in *O. ambulans*, none of the Slough Onychiuridae appear to avoid steady light. *O. ambulans* lives in earth, under stones and bark, and in caves (Handschin). Though widely distributed, it is more restricted than *O. armatus*. Frenzel did not find it in any of his meadows, but at Slough it is the most abundant species present. Ripper (1930) records it from mushroom beds. *Tullbergia quadrispina* occurs under stones and in humous soil (Handschin). Frenzel found it in three of his eight meadows, and notes that it is particularly deep-living. *T. krausbaueri* is much smaller than the other three species. They vary from 1 to 2·5 mm. in length, but *T. krausbaueri* does not exceed 1 mm. Handschin records it from humus, hot-houses, under flower-pots and under the damp bark of trees, in caves and on mushrooms. It is one of Frenzel's Leitformen, occurring in six of his meadows.

There is little information available on the life history of Onychiuridae. The most nearly related animal for which there is exact information is *Hypogastrura manubrialis* Tullb. The Hypogastruridae belong to the same superfamily, Poduromorpha, as the Onychiuridae. *H. manubrialis* has

attracted attention because it is a pest of mushroom beds, in which habitat it is sometimes accompanied by *O. ambulans* and *T. krausbaueri*. Its life history is summarized by Ripper (1930) as follows: the egg hatches in 19 days at 22° C., in 36 days at 10° C.

1st moult	...	...	7 days old
2nd moult	...	...	15 days old
3rd moult	...	...	22 days old
Sexual maturity		...	5–7 weeks
Total life-span		...	5–10 months

Moulting goes on throughout life, even after sexual maturity. Strebel (1932) gives similar figures for *H. purpurascens*. It would be extremely rash to assume that these figures are at all closely applicable to Onychiuridae, but they are the best information available and do show the type of life history which it is reasonable to expect.

2. Acknowledgements

This work has been done under the general direction of Prof. J. W. Munro. I am greatly indebted to Dr O. W. Richards, who supervised the work at every stage; and to Prof. F. G. Gregory, of the Plant Physiology Department of this College, who gave statistical advice and in particular devised the experiment on horizontal distribution. The late Dr W. Maldwyn Davies gave invaluable help, in the early stages, with the identification of Collembola.

3. Sampling

Sampling was carried out in the Pond Field at the Biological Field Station, Slough. This field had not been cultivated for at least ten years, and quite probably not for twenty, the only attention it received being annual hay-making. It is covered with coarse grass, cocksfoot (*Dactylis glomerata*) being very common. Couch grass (*Agropyrum repens*) is also present, as well as timothy grass (*Alopecurus pratensis*) and dock (*Rumex* spp.). There is a good deal of moss among the grass and other plants. The south side of the Pond Field is bounded by a stream, and the west side by a ditch which usually contains water only 2 or 3 ft. below the surface of the field. In a wet winter the water table rises almost to the surface.

As already mentioned, no attempt has been made to compile a complete list of the soil fauna, but some mention must be made of its more important characteristics. In numbers of individuals, Collembola comprised about 80% of the total fauna. Mites (Acarina) and Myriapods were of approximately equal abundance, the mites being concentrated at the surface, while the Symphyla (the most numerous Myriapods) are truly subterranean. Other Myriapods regularly present included Chilopods, both Lithobiidae and

Geophilidae, Diplopods and Pauropods. Larvae of Elateridae (Coleoptera), probably *Agriotes obscurus* Linn., were present in every sample, the numbers ranging from 3 to 33 per sample of 628 cu. in. (10·6 litres). Sometimes the larvae of crane-flies, *Tipula paludosa* Meig., occurred. The ant *Myrmica ruginodis* Nyl. occurred fairly regularly, and on one occasion (20 Sept. 1937) there were 95 in a single boring of 1180 c.c. The remainder of the fauna was composed of sporadically occurring animals such as the larvae of various Coleoptera and Diptera, nymphs of Hemiptera, thrips, spiders and earthworms.

In a patch of the Pond Field 80×50 ft. (24×15 m.) nine plots were marked out in a modified latin square. The three large plots SW, NC, EC, each 25×15 ft., were left quite undisturbed except that they were mowed twice each summer when the grass got inconveniently long, and it is with the samples taken from these plots alone that the present paper is concerned.

A sample consisted of 9 borings, 3 from each plot. Each plot was divided into imaginary 1 ft. squares, which were numbered consecutively. To determine the position of the borings, numbers were drawn at random from a box, a special box of numbers being kept for each plot. From a diagram was found the latitude and longitude of the centres of the squares so chosen, and the exact place to bore was then measured out on the plot and marked with a peg. This method ensured that the borings were placed at random, and that no boring could be less than a foot from the site of any previous boring. After the sampling, the holes were filled up with gravel.

The ideal size of a soil sample is closely bound up with the distribution in the soil of the various species being studied. Consideration of this matter is therefore deferred until after Section 5 on "Horizontal distribution".

The three borings from each plot were not washed separately, but mixed and passed through the machine together. More information would have been obtained had each boring been dealt with separately, but with the form of apparatus used this method would have been too laborious. The soil was a heavy clay containing very few stones. At about 13 in. a blue layer was encountered. The *p*H by Wulff strip-colorimeter method was $5{\cdot}0 \pm 0{\cdot}2$. A few simple constants were determined for the various layers:

	Ignition loss (%)	Moisture in air-dry soil (%)	Moisture in saturated soil (%)
4·5 in. (11·4 cm.)	14·05	5·944	96
4·5–9 in. (11·4–22·9 cm.)	10·78	5·942	58
9–13·5 in. (22·9–34·3 cm.)	9·82	7·650	58
13·5–16 in. (34·3–40·6 cm.)	8·37	6·040	—

The percentages refer to the dry weight of the soil. The estimate of the saturated moisture is only rough, and is derived partly from laboratory measurements by the rim method, which tries to use the soil undisturbed in the condition it was in in the field, and partly from soil-moisture determinations when the soil was water-logged. The top layer was very variable in this respect;

the rim, which is about an inch deep, pressed into the surface of the soil, has given values as high as 130%.

Ground temperatures at 75 cm., 25 cm. and 10 cm. are taken at 09.00 every morning at the Field Station. In October 1936 the 10 cm. readings were replaced by a distant recording thermograph with the sensitive bulb at 10 cm. All these temperatures were taken not on the sampling plots but some distance away, under short turf.

4. Technique

While many methods of separating insects from soil have been described, the flotation method of Ladell (1936) is for small animals so far superior to other methods that results obtained with it can be compared only with great caution to those obtained in other ways. A large Ladell's apparatus, considerably modified, was used. The mixing cylinder held 60 litres instead of 15, and the apparatus could take a 9-in. (23 cm.) cube (30–40 lb.) of soil at once. The size involved some modifications. A much stronger air current was used, and the turbulence induced by this was responsible for most of the stirring. A continuous mechanical stirrer was dispensed with, as occasional hand stirring was found to be sufficient. After passing across a settling tank the yield was caught in a Buchner funnel on a piece of 200 mesh Monel wire gauze. This holds animals just visible to the naked eye, but is very much quicker than filter paper and obviates the use of a suction pump.

It was a mistake to make such a big apparatus. It was begun because of a statement by Thompson (1924) that a 9-in. cube was a proper size for a soil sample. At that time I did not realize the advantages to be gained by subdividing and taking a composite sample composed of a number of smaller scattered ones. Actually the machine was scarcely ever used to capacity. In the ordinary way the size of a sample was 108 cu. in., which is exactly the size that Baweja regularly put into Ladell's original apparatus. Thus the greater capacity of my apparatus was unnecessary, while it was heavier to work and not so quick.

The product of these machines is a large quantity of vegetable debris in which the soil animals are entangled and from which they can be separated only by laborious hand sorting. The debris was washed off the wire gauze filter into a green photographic developing dish. This had a narrow level spout which came comfortably into the field of a binocular microscope with a magnification of $\times 140$. The debris was dragged into the spout with stout needles, vegetable matter allowed to fall and animals transferred to a watch-glass of 70% alcohol. This method seems superior to that of examining on the filter in strips or squares, as it is continuous and there is no need to stop searching in order to move the container. The separation of the animals from the vegetable debris is the longest and most tedious part of the process of

taking a soil sample, and one of the factors limiting the total amount of soil which can be examined. To bring a normal sample of 972 cu. in. (40–50 lb.) in from the field, wash it and sort it, usually took 4 days.

A second and in this case more important factor limiting the number of samples taken is the time taken to identify and count the animals. In previous soil studies large numbers of species have been identified and recorded as present, but the numbers of individuals of each species have not been recorded. The discussions of populations have referred to larger units such as families or orders. The distinction is important, because the identification of large numbers of Collembola, particularly, consumes a great deal of time. A certain number of specimens are bound to get damaged, and even when I had been identifying Onychiuridae for 18 months I sometimes found it necessary to use a magnification of 500 diameters to determine a damaged *Onychiurus*. The last sample taken on 16 October 1937 contained 1521 Onychiuridae, 694 other Collembola, 595 other animals. After the animals had been separated from the debris and brought into alcohol, to sort and count them and identify the Onychiuridae took 21 working hours. This was a fairly small sample and my speed was then much greater than it was earlier on. The sample taken on 16 September 1936, for example, contained 1230 Onychiuridae, 395 other Collembola, 948 other animals, and sorting, counting and identification occupied 35½ working hours. At times much larger samples had to be dealt with. Some of the Onychiuridae could be identified with binoculars as they lay in the alcohol, but most had to be transferred to lactic acid. After being cleared, the majority could be identified under a high power binocular, but a few had to be temporarily mounted on a cavity slide and examined with a monocular.

Each boring had an area of 8 sq. in. (52 sq. cm.). Early samples were taken to a depth of 9 in. (22·9 cm.), later samples to 13½ in. (34·3 cm.) and a few to 16 in. (40·6 cm.). A sample was composed of nine such borings, and all but three of the samples were divided into 4½ in. layers, for investigation of the vertical distribution of the fauna.

5. Horizontal distribution

Recent work of Blackman (1935), Ashby (1935) and others has drawn attention to the problem of the distribution of species in plant associations. Though a number of methods of describing plant associations have been developed which are based on the assumption that individuals of a species are distributed at random within the bounds of an association, it now appears that many species are not so distributed. Some are under-dispersed, that is, they tend to occur in groups or clumps; while others are over-dispersed: their distribution is more regular than a random distribution. In other words, an under-dispersed species tends to occur in aggregations, members of a randomly

dispersed species are indifferent to one another, but members of an over-dispersed species tend to be widely spaced in relation to their frequency.

The distribution of sessile and sedentary animals such as soil animals can be thought of in the same way as the distribution of plants, but the problem has attracted little attention. Jones (1937) in Washington found that some wireworms are distributed at random. Probably his populations of "wireworms" are composed of several different species, about whose distribution there is no information. Thompson (1924) performed an experiment which has since been taken to show (*a*) that the soil fauna is uniformly distributed (Ford, 1937*b*). (*b*) that a 9-in. cube is a satisfactory soil sample. The experiment consisted in counting the "Achorutidae" (a group including Onychiuridae, possibly equivalent to Poduromorpha) present in several series of samples, each of twenty 2-in. cubes. In some cases these were taken more or less at random, though similar vegetative coverings were selected for the sampling positions, in others they were taken along definite lines. The totals of these various series agreed closely, though the individual counts showed a wide range. From this it was concluded that a 9-in. cube, having the same area as twenty 2-in. cubes, "might be expected to give a reasonable picture of the Achorutid population of the soil as a whole, and that such a sample was a reasonable one on which to work in attempting to trace quantitatively the seasonal changes of the fauna".

This conclusion will not win support from anyone used to more modern statistical methods. It assumes that the variance over a whole field with an area of some 2000 sq. ft. will be no greater than that over 81 sq. in. But the fact that the numbers present in the small sampling units showed a great range is direct evidence that this is not so. Thompson's evidence shows that a sample of twenty scattered 2-in. cubes might be considered satisfactory, but not at all that one 9-in. cube would be satisfactory. Moreover, the distribution of the "Achorutidae" throws little light on the distribution of its constituent species, and none at all on that of other soil animals.

In the present investigation, it was unfortunate, from the point of view of the study of distribution, that the three borings taken from each plot in a routine sample were mixed together. Had separate counts from each boring been available, it would have been possible to test the distribution by means of the Poisson series. But as this was impossible, a special experiment was devised. This was a sample consisting of nine pairs of borings, three pairs at random on each plot, and the members of a pair touching. Then, in a species distributed at random in the soil, the number of individuals present in one member of a pair of borings should be independent of the number in the other. If on the other hand the species is under-dispersed, in aggregations, the two counts from a pair of borings should be correlated, while in an over-dispersed species they should be negatively correlated.

The first experiment on the distribution of the animals was made on

11 November 1936. The two members of a pair of borings were taken in quick succession, the first hole being stopped with a cylinder of a size to prevent the wall crumbling. The borings were taken to 9 in. only, and not divided into layers as usual. The following counts are given in their plots, and the two members of a pair are designated West and East respectively.

When the variance of this material is analysed, it is found that in each of the four species the variance between pairs was significantly greater than the variance within pairs. In other words, all four species occur in aggregates. The result is highly significant, exceeding the 0·001 level of significance in every case except that of *T. quadrispina*, in which case P is 0·05–0·01. The four species considered together are also aggregated, P 0·05–0·01. The moisture and ignition loss appear to be distributed at random.

Having established that the animals occur in groups, it is of interest to know the size of the groups. In the last experiment the centres of the borings were 3 in. apart (the diameter of the borer) so that the size of the aggregations must be of at least this order. Repetition of the experiment with the members of each pair increasingly far apart should discover the upper limit of size of the aggregations, for if the members of a pair are taken a distance apart much greater than the size of the aggregations, the aggregations will not be detected and the animals will appear to be distributed at random. The experiment was accordingly repeated on 20 September 1937, taking the members of each pair 1 ft. apart.

Here, in the case of *O. armatus* there is no difference in variance within pairs and between pairs. In the case of the other three species there is a significant difference, which for *O. ambulans* P is less than 0·001, for *T. quadrispina* and *T. krausbaueri* P is 0·01–0·001. For the last three species considered together the difference is very significant, P being less than 0·001, while for all four species considered together the difference is less significant, P 0·05–0·01. This means that if *O. armatus* is aggregated the aggregations are less than a foot in diameter, so that they are not detected by this experiment. But the other species are grouped in aggregations a foot or more across, while the moisture and that property measured by ignition loss lie in patches of the same order of size.

We may now enquire into possible causes of this irregular distribution. For each boring the moisture content, ignition loss and *p*H value were determined. These constants were selected because they are factors which might reasonably be expected to affect soil animals and are also easy to determine. They by no means exhaust the list of possible soil physical factors which may be important. The *p*H value was so constant that its influence was discounted. Correlation coefficients were calculated between the numbers of each of the four species and the measurements of each of the physical factors. This was done separately for the data in Table 1 and Table 2. In some cases the correlations on these two dates were very different, and it was thought that this might be due to the soil being very much wetter on the first occasion.

Confirmation of this supposition was sought from the routine samples. Of these there

Table 1. *Distribution of Onychiuridae on* 11 *November* 1936.
Members of random pairs touching

	Onychiurus armatus		*Onychiurus ambulans*		*Tullbergia quadrispina*		*Tullbergia krausbaueri*		4-spp. total		Moisture		Ignition loss	
	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.
SW	34	61	17	21	37	53	14	13	102	148	48·73	54·00	15·48	13·52
	5	9	35	48	9	6	2	5	51	68	50·36	56·24	13·03	14·38
	17	13	148	114	18	7	7	9	190	143	50·84	52·37	12·18	11·94
NC	18	4	29	20	9	13	101	90	157	127	49·76	49·97	13·07	13·89
	32	16	37	10	20	5	21	7	110	38	54·01	45·26	12·72	11·65
	11	7	9	4	25	15	26	25	71	51	49·56	50·39	11·92	12·62
EC	29	18	78	107	13	20	19	38	139	183	55·56	50·28	12·59	13·57
	65	72	49	65	28	45	12	12	154	194	58·43	55·49	12·79	11·94
	12	3	109	62	36	21	36	46	193	132	54·98	52·61	8·46	11·75

Mean moisture 52·16%, mean ignition loss 12·67%

Table 2. *Distribution of Onychiuridae on* 20 *September* 1937.
Members of random pairs 1 *ft. apart*

	Onychiurus armatus		*Onychiurus ambulans*		*Tullbergia quadrispina*		*Tullbergia krausbaueri*		4-spp. total		Moisture		Ignition loss	
	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	E.
SW	18	5	56	60	12	2	14	11	100	78	42·81	35·08	11·65	10·26
	13	15	37	46	2	8	10	7	62	76	34·06	42·66	9·98	12·25
	14	27	107	174	18	21	12	7	151	229	46·01	48·71	11·83	11·61
NC	11	12	28	25	19	17	7	23	65	77	34·15	33·86	10·47	12·47
	15	36	8	27	16	3	59	41	98	107	32·63	35·28	9·86	10·39
	18	32	5	2	44	69	21	24	88	127	31·77	30·65	12·30	11·48
EC	24	56	0	1	16	11	13	6	53	74	53·65	41·93	13·11	14·03
	13	7	35	26	16	4	21	13	86	50	42·85	41·26	14·41	13·25
	35	55	6	3	6	9	9	16	56	83	33·10	39·51	10·90	11·44

Mean moisture 39·53%, mean ignition loss 12·06%

were 23, for each of which counts were available from each of the three plots, together with moisture determinations and, in most cases, ignition losses. The raw data is given in the Appendix. For the whole series the mean moisture content was 47%. In 10 samples the moisture content lay above the mean, and in 13 below. These two groups of routine samples were then treated separately as "drys" (13 samples, mean moisture content 38·97%) and "wets" (10 samples, mean moisture content 52·16%). To obtain correlation coefficients from the data given in each of Tables 1 and 2 no allowance need be made for fluctuations in populations at different times of the year. But when different dates are combined it is necessary to eliminate the effect of population fluctuations, if, as at present, we are concerned only with spatial distribution. To do this, the numbers of each species in any plot were expressed as a percentage of the total numbers of that species in all plots on that date, and this percentage was used to derive the correlations between numbers and the physical factors measured. These correlations therefore concern spatial distribution only and are not affected by population changes.

Partial correlations between percentage numbers of insects, percentage content and percentage ignition loss were separately calculated for the "wets" and the "drys". In most cases the differences between the wets and the drys confirmed the differences between the wet sample of 11 November 1936 and the dry sample of 20 September 1937. In the following table, the column P indicates the level of significance. Where no value of P is given the correlation is not significant (P exceeds 0·05).

Table 3. *Partial correlations—horizontal distribution*

	11 Nov. 1936 mean moisture 52·16%		Wets mean moisture 56·98%		20 Sept. 1937 mean moisture 39·53%		Drys mean moisture 38·97%	
		P		*P*		*P*		*P*
Moisture-ignition loss	−0·1446	—	0·2911	—	0·5930	0·02–0·01	0·4402	0·02–0·01
Onychiurus armatus-moisture	0·5335	0·05–0·02	0·5254	0·01	0·0174	—	−0·0410	—
Onychiurus armatus-ignition loss	0·2220	—	−0·1052	—	0·1171	—	0·0938	—
Onychiurus ambulans-moisture	0·2748	—	0·2767	—	0·5504	0·05–0·02	0·5059	0·01
Onychiurus ambulans-ignition loss	−0·3733	—	0·0109	—	−0·3579	—	−0·3047	—
Tullbergia quadrispina-moisture	0·3310	—	−0·1612	—	−0·3926	—	0·6418	0·01
Tullbergia quadrispina-ignition loss	−0·0327	—	0·1440	—	0·3245	—	−0·5586	0·01
Tullbergia krausbaueri-moisture	−0·2205	—	−0·2186	—	−0·2742	—	−0·2638	—
Tullbergia krausbaueri-ignition loss	−0·0037	—	0·1684	—	−0·1041	—	0·1032	—
4 spp.-moisture	0·4145	0·1	0·1966	—	0·4093	—	0·2304	—
4 spp.-ignition loss	−0·2430	—	0·0155	—	−0·3425	—	0·2238	—

In certain cases in this table the values for 20 September 1937 and the drys, though not separately significant, can be combined to give a significant value. In some cases where all four values, both wet and dry, are insignificant but much the same, they can be combined to give a significant value.

Table 4. *Combined partial correlations—horizontal distribution*

	Drys		All values	
		P		*P*
Onychiurus ambulans-ignition loss	−0·3426	0·05–0·02	—	—
Tullbergia krausbaueri-moisture	—	—	−0·2468	0·05
4 spp.-moisture	—	—	0·3055	0·01

From these tables the following facts emerge. The numbers of *O. armatus* are positively correlated with moisture in the wet season, but are indifferent in the dry. From this it need not be inferred that *O. armatus* has some unusual hydrophilic response to very wet soil. It is more likely that it is attracted by some other soil factor which happens to be associated with the wet patches. It is worth recalling that Fidler (1936) found that with chafer larvae there is a steady rise in the tolerated temperature as the soil water increases up to 60% saturation, though above this point there is a rapid decrease. Some similar relationship might easily account for the at first sight peculiar response of *O. armatus*. On the other hand, *O. armatus* is not to be regarded as drought-hardy from its indifference to moisture in the dry season. The soil moisture at no time fell below 29%, and it is probable (Keen, 1931, p. 290) that the moisture content of such a soil would have to fall well below 10% before the soil atmosphere ceased to be saturated.

The numbers of *O. ambulans* are correlated with soil moisture in the dry season, but cannot be shown to be so in the wet. In the dry season they are negatively correlated with ignition loss. *T. krausbaueri* appears to be unaffected by the seasons and to avoid moist places at all times. The four species considered together, on the other hand, show a positive correlation with moisture when all values are combined. The position of *T. quadrispina* is anomalous. Whereas in the three other species the "wets" value has agreed with that for

11 November 1936, and the "drys" value with that for 20 September 1937, in *T. quadrispina* this is not so. The correlations with both moisture and ignition loss differ in sign in each case, and the differences between 20 September 1937 and the "drys" are very significant, though the differences between 11 November 1936 and the "wets" are not significant. This discrepancy is quite extraordinary and no explanation can be offered.

From these correlations we see that no two of the four species have the same reactions to moisture and ignition loss, and that the reactions of the four species considered together are not a guide to the reactions of any one species. The correlations do not at all explain the aggregations present on 11 November 1936, for at that time both moisture and ignition loss appeared to be randomly distributed. But on 20 September 1937 moisture and ignition loss were correlated and in patches. *O. armatus* was indifferent to both of them and was distributed at random. *O. ambulans* was positively correlated with moisture, negatively but less strongly with ignition loss, and apparently the effect of moisture dominates and it is strongly aggregated. *T. quadrispina* behaves anomalously. *T. krausbaueri* is negatively correlated with moisture and so presumably gathers in dry places.

Thus the wet weather aggregations are not explained by reactions of the animals to moisture or ignition loss. The dry weather aggregations may be partly so explained, though it is probable that even here the explanation is far from complete. It is unfortunate that the two samples were taken such a long time apart, for there is no evidence that *O. armatus* was not in aggregations over a foot in diameter on 11 November 1936, or that it was in small aggregations on 20 September 1937. All that we can say is that *O. armatus* was in aggregations of the order of 3 in. diameter on 11 November 1936, and that on 20 September 1937 it was not in aggregations of the order of 12 in. diameter.

An investigation of the effects of liming the soil, on some sample plots, showed that on the whole liming had little influence on numbers. On application of the z and t tests, it was found that only in the case of *T. krausbaueri* was the effect of liming significant (P 0·02–0·01). For the other three species and for the four species together, there was not a significant difference between the limed and the unlimed plots.

6. Choice of sample size

In any investigation involving sampling a large population, there is always a conflict between the ideal of a high degree of accuracy and the labour involved in attaining that ideal. This conflict can best be resolved by studying the most efficient way of using a given amount of labour, and the increase of accuracy to be gained at any time by increasing the labour. Thus, if only a certain time is available for taking one sample, the sampling should be so planned as to give the most accurate possible estimate of the population, and at the same time the most accurate possible statistical estimate of the accuracy attained. On the other hand, if the time for sampling is not strictly limited, it should be ascertained whether or not an increase in size of sample will be accompanied by a proportionate increase in accuracy. For example Jones (1937) was able to show that, in sampling certain wireworm populations, very little additional accuracy was obtained by taking a sample of 100 units, instead of one of 50 units, although 50 units were very much more accurate than 25. In other, denser, populations it was necessary to take only 30 units, for the extra

accuracy obtained by taking more was not commensurate with the additional labour involved.

In the present investigation the three borings taken from any plot on any occasion were mixed and then put through the Ladell's apparatus together. This saved a good deal of labour, and did not affect the real accuracy of the resultant figures for the population. On the other hand it did seriously affect the statistical estimate of the accuracy, and in this way was responsible for considerable loss of information. But when the experiment was planned it was decided to sacrifice this information in order that the samples could be stratified and the vertical distribution studied. As it turned out, the information gained on vertical distribution was probably less interesting than the information lost on horizontal distribution, but there was, of course, no means of knowing this beforehand.

On two occasions, however, separate counts for each boring are available for each of the four species studied. From these data (Tables 1 and 2) the relative standard error has been calculated, by expressing the standard error as a percentage of the mean, the standard error being calculated from the formula

$$\text{S.E.}^2 = \frac{\sigma^2}{N}$$

where σ is the standard deviation, and N the number of units in the sample. As explained, although 18 borings were taken on each of these occasions, they were not 18 independent borings, but 9 random pairs. It is therefore not possible to calculate the standard error with $N = 18$, but only for two parallel series in each of which $N = 9$. In the sample taken on 11 November 1936 (but not in that of 20 September 1937) the two members of a pair of borings were touching. It is therefore possible to regard them together as a single sample of area 16 sq. in. (103 sq. cm.). Moreover, by substituting other values of N in the formula, it is possible to estimate the accuracy obtainable by increasing the number of units in the sample. Table 5 gives the relative standard errors, calculated from the data in Tables 1 and 2, of the west members of the pairs, the east members of the pairs, and in the case of the sample on 11 November 1936, the pair totals. Besides the actual standard error is given the estimate of what the standard error would be if the number of borings were increased to 16 or 25. The standard error is an expression of the accuracy of the mean of a sample. It implies that the true population lies within the limits of the mean plus or minus twice the standard error.

These high relative standard errors proceed directly from the very irregular distribution which has already been discussed. It is noticeable that increasing the number of units in the sample would greatly increase the accuracy of the estimate of the population of each of the four species, but when they are considered together as Onychiuridae, 25 borings would be little better than 16, and 16 not a great deal better than 9. It is also noticeable that doubling the

size of the sampling unit (as in the row "W.E. total") has very little effect on the accuracy: it is possible that a smaller unit would be nearly as accurate. But *Onychiurus ambulans* is so irregularly distributed that although on 20 September 1937 it had the highest mean population of any Onychiuridae, it was entirely absent from one of the borings. If the size of the sampling unit were decreased too much the number of zero counts might increase rapidly, and this would lower the accuracy considerably.

Table 5. *Relative standard errors, from data of Tables* 1 *and* 2

Date	Series	*N*	*Onychiurus armatus*	*Onychiurus ambulans*	*Tullbergia quadri-spina*	*Tullbergia kraus-baueri*	Onychiuri-dae
11 Nov. 1936	W.	9	21·89	23·02	15·53	29·54	11·19
		16	16·42	17·27	11·64	22·16	8·39
		25	13·13	13·81	9·32	17·73	6·71
	E.	9	34·61	18·18	25·03	28·97	10·18
		16	25·95	13·63	18·73	22·65	7·64
		25	20·76	10·91	14·99	18·11	6·11
	W.E.	9	27·52	19·64	18·73	29·02	7·90
	total	16	20·64	14·73	13·75	21·76	5·91
		25	16·51	11·78	11·00	17·41	4·74
20 Sept. 1937	W.	9	11·03	22·73	18·43	25·00	10·10
		16	8·28	17·05	13·82	18·76	7·58
		25	6·62	13·64	11·30	14·50	6·06
	E.	9	20·89	30·04	37·80	11·74	10·85
		16	15·66	22·53	28·35	8·78	12·63
		25	12·53	18·03	22·68	7·02	10·11

It is not possible to generalize on the subject of the ideal size of a soil sample. The best size and composition of a sample to take will be dependent upon the population to be studied, the character of the soil, and in particular upon the information which is being sought.

7. Vertical distribution

In Table 6, the figures for the upper two layers are the means of 20 samples, those for the third layer the means of 15 samples, weighted to make them correspond with the others. Those for the bottom layer are derived from only three partial samples, equivalent to one whole sample.

Table 6. *Mean vertical distribution of Collembola*

Depth in.	*Onychiurus armatus*	*Onychiurus ambulans*	*Tullbergia quadrispina*	*Tullbergia krausbaueri*	"Other Collembola"	All Collembola
0–4·5	151	181	66	101	320	819
4·5–9	73	185	82	54	67	461
9–13·5	30	117	68	25	28	268
13·5–16	2	36	36	11	2	67

Fig. 1 shows these distributions graphically. It emphasizes the distinction already insisted upon, between Onychiuridae as subterranean animals and other Collembola as surface dwellers. Actually it is probably not quite an accurate picture of the distribution of "other Collembola". The lower layers

were sampled by putting the borer back in the hole left after taking the upper sample. The hole was thus left open for a few minutes, during which time nothing was done to prevent Collembola from the surrounding vegetation from jumping into it. When the lower layer was removed such Collembola would, of course, be recorded as belonging to that layer. Thus the circumstance that the technique was not specially planned to deal with "other Collembola" has produced in these animals the appearance of a deeper distribution than they really have.

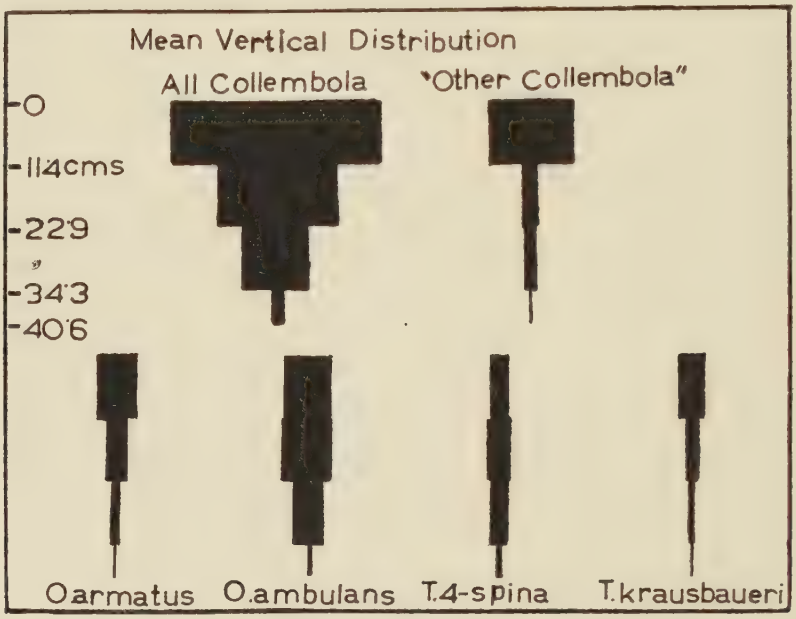

Fig. 1.

Fig. 1 emphasizes once more the differences which exist between closely related species. *Tullbergia quadrispina* is almost equally abundant in the first three layers. Frenzel (1936) also found that it had a remarkably deep distribution, and that at a depth of 15–25 cm. it was the sole representative of the order.

Onychiurus ambulans makes considerable migrations, and is only rarely in the mean condition of Fig. 1. The other three species always kept approximately to the distribution shown. Fig. 2 shows the seasonal migrations of *O. ambulans*. With it are plotted the saturation deficiency of the soil in three $4\frac{1}{2}$-in. layers, and the soil temperatures at 10 cm. and 75 cm. depth. The saturation deficiency is a measure of the dryness of the soil. The value is obtained by subtracting the moisture content at the time from the moisture content when the soil is saturated. Since the saturation point of the upper

soil is much higher than that of the lower, equal values for the moisture content correspond to a much higher saturation deficiency in the upper layer.

The seasonal migrations of *O. ambulans* are not extensive, that is to say, at no time does it completely vacate a layer in which it is abundant at another time, but it does have a distinct tendency to live at greater depths in summer and winter than it does in spring and autumn. It is not very easy to relate this movement to physical changes. It seems reasonable to suppose that the downward trend in summer is in search of greater moisture, for in considering

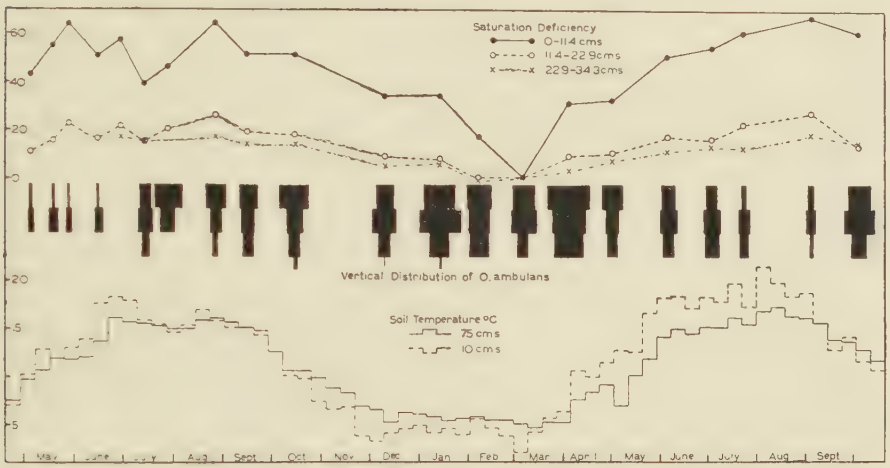

Fig. 2.

the horizontal distribution a correlation was found between this species and moisture in dry conditions. But the two cases are not necessarily comparable. When one layer of soil is damper than another it is a simple reversible difference with no further implications; but when one patch of soil is damper than another a few feet away it is likely to be associated with other differences. We know it is in fact associated with differences in ignition loss, and have eliminated the effect of this factor, but we do not know whether it is associated as well with some other factor such as pore-space. However, in the absence of any other information it seems reasonable to suggest that the summer descent may be a response to surface dryness.

It seems unlikely that moisture is important in the winter descent. It is noticeable that all the time the animals are in the winter deep position the deep temperature exceeds the shallow temperature. On the other hand no correlation was found (see below) between temperature and the populations of *O. ambulans*. Still, it is quite possible that *O. ambulans* does become sensitive to temperature when the temperature is low, for if such a relation did exist it would occur in too few of the samples to be apparent in the general correlation. So it is suggested that when, in winter, the surface of the ground becomes cold, *O. ambulans* tends to descend to where it is warmer.

Frenzel (1936) could not detect vertical movements in any of the groups of animals in his meadow. Bryson (1935) found that wireworms in Kansas moved down in summer and in winter, just as *O. ambulans* does, and ascribed the movement to temperature in each case. McColloch & Hayes (1923) found that white grubs and May beetles moved down in winter and up in summer, so that they were always in the warmer layer.

8. Population fluctuations

Samples were taken during the 19 months from April 1936 to October 1937. The results of these samples are given in Figs. 3 and 4. All the curves refer to the population to a depth of 9 in. (23 cm.) as the early samples were taken no deeper than this. Inclusion of the 9–13½ in. layer would not have affected the general character of the curves, except to increase the relative heights of the peaks of *O. ambulans*.

From the data were calculated correlation coefficients between the populations and the soil temperature and the soil moisture. As the soil moisture is strongly correlated with temperature, it was important to eliminate the effect of each of these variables when considering the other. Table 7 gives the partial correlations of the populations, with temperature with the effect of moisture eliminated, and with moisture with the effect of temperature eliminated. The temperature is the soil temperature at 25 cm., the value being the mean of the readings for the 100 days before the sample was taken.

Table 7. *Partial correlations of populations with soil moisture and temperature* (100 *day mean*). *The value of* P *is given where it is* 0·05 *or less*

	Moisture	*P*	Temperature	*P*
Onychiurus armatus	0·5783	0·01	0·5825	0·01
Onychiurus ambulans	0·4782	0·05–0·02	0·3113	—
Tullbergia quadrispina	0·2193	—	−0·0093	—
Tullbergia krausbaueri	0·4707	0·05	0·4603	0·05–0·02
Onychiuridae	0·6317	0·01	0·5301	0·01
Three species*	0·5516	0·01	0·5351	0·01
"Other Collembola"	−0·0431	—	0·6022	0·01
Moisture-temperature (total correlation)	−0·6319	0·01	—	—

* A total of *O. armatus, T. quadrispina, T. krausbaueri.*

Correlations were also calculated between the populations and the temperature means for 56, 28 and 14 days before sampling. The values obtained have, of course, different values for the partial correlation with moisture, and generally speaking neither were significant. Table 8 gives the few partial correlations which were significant, based on the mean temperature of 56 or 28 days. None of the partial correlations based on the mean temperature of the previous 14 days were significant.

The temperature correlations increased, the greater the mean number of days for which they were calculated. The partial correlation coefficients of

Table 8. *Partial correlations of populations with soil moisture and temperature (means of 56 and 28 days)*

	Moisture	*P*	Temperature	*P*
(*a*) Mean temperature of previous 56 days				
Onychiurus armatus	0·5676	0·01	0·5437	0·01
Three species*	0·4484	0·05–0·02	—	—
(*b*) Mean temperature of previous 28 days				
Onychiurus armatus	0·4745	0·05–0·02	0·4200	0·05
Three species*	0·4474	0·05–0·02	—	—

* Total of *O. armatus*, *T. quadrispina*, *T. krausbaueri*.

T. krausbaueri, a typical case, for the temperature means of the previous 14, 28, 56 and 100 days were respectively 0·0718, 0·1781, 0·3324, 0·4603. Thus, with certain exceptions, there is a significant partial correlation between each species and moisture and temperature. The exceptions are *O. ambulans*, which is not significantly correlated with temperature, the group "other Collembola" which is not significantly correlated with moisture, and *T. quadrispina*, which is not significantly correlated with either. It is worth recalling at this point the limitations of the statistical method. Absence of proof of a proposition does not imply proof of the converse. The partial correlations *O. ambulans*-temperature (0·3113) and *T. quadrispina*-moisture (0·2193) are not significant, but at the same time they are not significantly different from the corresponding correlations of *O. armatus*. That is to say the evidence available is not sufficient to enable one to say that the populations of *O. ambulans* and *T. quadrispina* are correlated differently from that of *O. armatus*, and it is quite possible that a more thorough investigation comprising a greater number of samples would reveal a significant correlation both for *O. ambulans*-temperature and *T. quadrispina*-moisture. On the other hand the partial correlations *T. quadrispina*-temperature and "other Collembola"-moisture are significantly different from the corresponding correlations of *O. armatus*. Though one cannot affirm that these populations are indifferent to temperature and moisture respectively, one can say that their relation to these factors is different to that of *O. armatus*, which can be specified. Further investigation might reveal a positive correlation, though this would have to be very small to fulfil the condition of difference from *O. armatus*, or a negative correlation; but since the observed correlations are so nearly zero, there is a presumption (but only a presumption) that within the limits of the observations *T. quadrispina* is indifferent to temperature, and "other Collembola" to moisture.

The partial correlations of Table 7 above are not, however, of great assistance in interpreting the population fluctuations shown in Figs. 3 and 4. This is on account of the large negative correlation between temperature and moisture. In practice these two factors almost entirely cancel one another out.

Table 9 shows the result of calculating the total correlation of the populations with moisture and temperature without eliminating the effect of these

variables upon each other. We see that in the majority of cases these two factors have interfered with each other to such an extent that we can no longer regard their influence as being significant. A period of high temperature, which favours the animals, coincides with drought which inhibits them, and vice versa. Exceptions to this are the Onychiuridae, and the "other Collembola". The Onychiuridae show a positive total correlation with moisture, and Fig. 3 demonstrates how they are at a maximum in the wet season and fewer in the dry (see Fig. 2). Actually the minimum of Onychiuridae, as of all other groups, was in April 1936, which was not a dry period. This phenomenon will be discussed later.

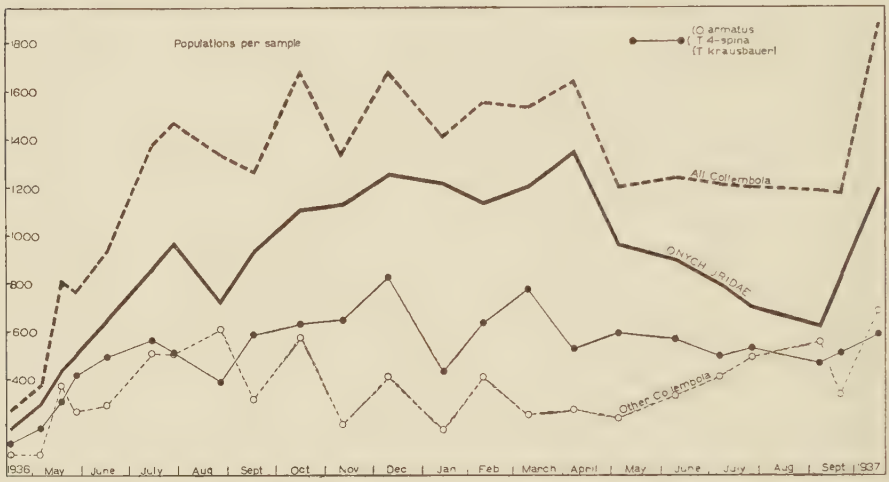

Fig. 3.

Table 9. *Total correlations of populations with temperature* (100 *day mean*) *and soil moisture*

	Moisture	*P*	Temperature	*P*
Onychiurus armatus	0·2594	—	0·2721	—
Onychiurus ambulans	0·3824	—	−0·0187	—
Tullbergia quadrispina	0·2852	—	−0·1872	—
Tullbergia krausbaueri	0·1541	—	0·2551	—
Onychiuridae	0·4175	0·05	0·1095	—
Three species*	0·2736	—	0·2261	—
"Other Collembola"	−0·4720	0·05–0·02	0·7097	0·01

* Total of *O. armatus*, *T. quadrispina*, *T. krausbaueri*.

"Other Collembola" are positively correlated with temperature and negatively with moisture, so they should be most numerous in summer. Their curve on Fig. 3, in spite of violent fluctuations, tends to an autumn peak and a spring minimum. Since the temperature relation is a long-term effect, the violent fluctuations which are so noticeable from August to February cannot be due to this cause. The effect of moisture (Table 9) is apparent, not real (Table 7) so that this factor is not responsible either. Analysis of the population

fluctuations of Onychiuridae makes one disinclined to press any further enquiry into the causes of fluctuations in the wide and indefinite group "other Collembola".

Fig. 4 shows that the four species of Onychiuridae, which have already been shown to be so different with respect to horizontal and vertical distribution, are also extremely different with respect to population fluctuations. The most striking case is that of *Onychiurus ambulans*, whose peak population is thirteen times the minimum, while the peak of the Onychiuridae as a whole is only seven times the minimum. It was shown in Table 7 that *O. ambulans* was correlated with moisture, but not that it was correlated with temperature. The assumption that moisture was more important to it than temperature

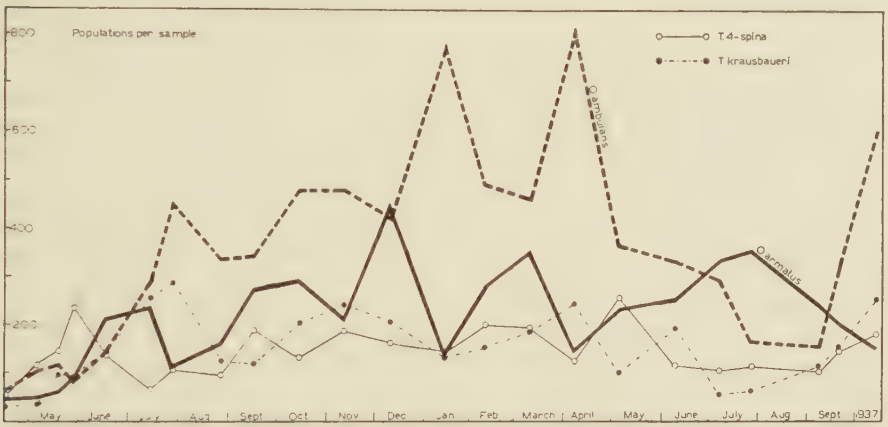

Fig. 4.

Table 10. *Soil temperature at 25 cm.: means of preceding periods*

	14 days	28 days	56 days	100 days
20 Apr. 1936	5·13	6·29	5·13	3·93
5 May 1936	7·56	6·37	6·32	4·67
18 May 1936	10·88	9·12	7·78	5·64
28 May 1936	12·11	11·00	8·48	6·76
16 June 1936	12·54	12·11	10·78	8·62
14 July 1936	16·36	16·48	14·29	11·46
28 July 1936	15·23	15·79	15·18	12·88
27 Aug. 1936	15·84	15·48	15·60	14·77
16 Sept. 1936	15·04	15·51	15·34	15·52
15 Oct. 1936	8·23	11·01	13·20	14·19
11 Nov. 1936	7·44	8·34	9·78	12·28
10 Dec. 1936	4·60	5·49	6·88	9·34
13 Jan. 1937	4·82	4·94	4·79	6·17
10 Feb. 1937	4·36	4·54	4·74	5·08
10 Mar. 1937	2·94	3·71	4·13	4·34
7 Apr. 1937	4·46	4·03	3·88	4·19
5 May 1937	9·23	8·75	6·35	5·32
9 June 1937	14·57	12·66	10·88	7·84
7 July 1937	15·43	15·28	13·97	11·23
27 July 1937	16·22	15·74	15·40	13·18
7 Sept. 1937	16·20	16·80	16·65	15·99
20 Sept. 1937	14·10	15·18	16·10	15·86
16 Oct. 1937	11·05	11·69	13·51	14·88

would account for the high winter populations of this animal, which at other seasons was not more numerous than other Onychiuridae.

The peak of *Onychiurus armatus* is ten times the minimum. As with *O. ambulans* its maximum occurs in winter. Both in 1936 and 1937 it had another peak in July. This species has a high partial correlation with both temperature and moisture, and taken over the whole period these two factors nullify one another (Table 9). But lacking knowledge of the moisture reactions at low temperatures or the temperature reactions at low moistures, we cannot deny that these factors may be responsible for the winter and summer peaks respectively.

Tullbergia quadrispina at its peak is only five times its minimum. It has a peak in May followed by a depression in July, August and September of both years. From October to April the population is steady. This is the only species showing no significant correlation with either moisture or temperature, and this is reflected in the fact that it is in numbers the least variable species. *Tullbergia krausbaueri* has a peak ten times its minimum. The peaks occur about every four months, in July, November, April, June and October. This species has a significant partial correlation with both moisture and temperature, but taken over the whole period these two factors cancel each other out, and as with *O. armatus*, it is impossible to say whether a more detailed knowledge of the temperature-moisture reactions would do much to explain these population fluctuations, or whether other factors are mainly responsible. The three species *O. armatus*, *T. quadrispina* and *T. krausbaueri* agree in having a low January population, and their populations are in general not dissimilar during the winter months. The curve of the total of these three species (Fig. 3) has a pronounced double winter peak, with an intervening minimum in January. By the *t* test the January population is significantly less than the mean of the December, February and March populations (*P* 0·05–0·02). The double peak in this curve can therefore be regarded as significant, unlike the conspicuous double peaks in the curves of *O. armatus* and *O. ambulans*. In neither of these cases are the minima significantly less than the surrounding peaks.

Review of the literature led Ford (1937*a*) to the tentative conclusion that such a double winter fluctuation as we have here in the combined population of *O. armatus*, *T. quadrispina* and *T. krausbaueri* is a general characteristic of populations of Collembola. The data present here are favourable to Ford's hypothesis, but do not offer it any strong support. The significant dip in the "three species" curve cannot be regarded as very important, for we have no good grounds for grouping these three species together. As already noted, the dips in the curves of *O. armatus* and *O. ambulans* cannot be regarded as significant.

In February and March, as shown in Fig. 2, the ground was extremely wet, and in March became completely waterlogged. The holes left after

sampling filled up with water, pools of water lay about on the plots. The Onychiuridae were apparently unaffected by this flooding. Ordinarily it is impossible to wet the animals with water: it is possible that they carried an air-bubble round them throughout the flooded period. In February 5·31 in. of rain fell, in March 3·08. This rain, which was well distributed, would probably keep the soil water fairly well aerated. Ingram (1931) by flooding was able to exterminate soil animals, including *Onychiurus armatus*, in sugar-cane fields, but doubtless high temperatures obtain in Louisiana.

As samples were taken during only 19 months, it is not possible to say much about annual, as opposed to seasonal, population fluctuations. But it is remarkable that the only feature which all the Onychiuridae have in common, and in which they agree with "other Collembola" is that their minimum was in April 1936. The winter of 1935–6 was colder than that of 1936–7 and the surface of the ground was for some time frozen solid to a depth of several inches. Probably this cold reduced the whole Collembolan population.

It has been the custom to express soil populations in millions per acre. When at their peak the Onychiuridae reached a density of 117 millions per acre. This statement gives a false impression of enormous abundance. It actually implies a density of one animal to 8 c.c. of soil, of which 20–40% can be regarded as habitable pore-space. The custom of expressing population densities with reference to area can be extremely misleading, and greater care should be taken to refer them to the real environment. Thus Baweja, in his study of recolonization after soil sterilization, refers (his Table 12) populations to area, and records for Collembola an increase of 1·6–2·2 over the control. Yet elsewhere (p. 92) he records that Onychiuridae failed to regain their normal strength. The Onychiuridae are soil dwellers and two populations may perhaps be legitimately compared on an area basis. But the other Collembola, such as Hypogastruridae, Entomobryidae and Isotomidae, live in the bottom of the vegetation. Their population density must be calculated on a basis which makes allowance for the density of that vegetation. Baweja's photographs show that there was a very much stronger growth of vegetation on his sterilized plots than on the controls, owing to the effect of heat sterilization on the soil. In other words there was more vegetation for the Collembola to live on. Had he made allowance for this by calculating the population density on some such basis as the weight of vegetation per sample, it is quite possible he would have found no difference in density between experiment and control.

The highest density of population per unit volume is summarized in Table 11. None of these are very high populations in the absolute sense. Park (1938) for instance, found 32 g. of flour supporting 89 live *Tribolium confusum*, or nearly 3 per gram, an incomparably denser population, in terms of biomass, than anything present in the soil. The figures in columns A, α–γ, represent the density in the areas of maximum population density. As they are derived from the totals of three independent borings, higher densities

than those shown no doubt actually occur. These figures may probably be halved to give a fair estimate of the number of c.c. supporting one animal, in the closest aggregations found.

Table 11. *Number of cubic centimetres of soil containing one animal*

A, maximum recorded density from any plot at any time.
B, peak population, mean of largest sample.
C, mean population.
D, minimum population.

α, 0–11·4 cm.
β, 11·4–22·9 cm.
γ, 22·9–34·3 cm.

	A			B			C			D		
	α	β	γ	α	β	γ	α	β	γ	α	β	γ
Onychiurus armatus	7	20	35	15	61	204	35	73	177	183	253	—
Onychiurus ambulans	6	7	12	12	15	18	29	29	45	379	74	—
Tullbergia quadrispina	23	18	19	36	47	50	80	65	78	279	113	190
Tullbergia krausbaueri	20	24	61	27	59	—	53	98	212	83	156	—
Onychiuridae	4	6	8	7	9	13	11	13	22	36	35	—

9. Summary

1. Samples were taken from a coarse long-neglected meadow at Slough at intervals over 19 months. The fauna was separated by means of a large Ladell apparatus. In the truly subterranean fauna the most important group was the Onychiuridae, of which there were four species, *Onychiurus armatus*, *Onychiurus ambulans*, *Tullbergia quadrispina* and *Tullbergia krausbaueri*.

2. None of the four species is distributed at random in the soil. All are aggregated, the size of the colonies being for *O. armatus* about 3 in. diameter, for the other species at least 12 in. diameter. Under wet conditions the distribution of *O. armatus* is positively correlated with soil moisture, and under dry conditions *O. ambulans* is positively correlated with moisture, and negatively with the ignition loss of the soil. The correlations do not fully account for the uneven distribution of the animals.

3. It is shown that owing to the uneven distribution of the animals, it is necessary to take a sample composed of a large number of small units, in order to get an accurate estimate of the population.

4. The vertical distribution of each of the species is different. *O. ambulans* and *T. krausbaueri* are most numerous near the surface, their numbers falling off gradually. *T. quadrispina* is evenly distributed to a depth of $13\frac{1}{2}$ in. (34·3 cm.) below which depth it is more rare. *O. ambulans* shows seasonal changes in vertical distribution, in spring and autumn it is most plentiful near the surface, while in summer and winter it is more abundant deeper down. It is suggested that the summer alteration is occasioned by dryness, the winter by temperature.

5. The populations of each species show positive partial correlations with soil moisture and temperature, except in the case of *O. ambulans*, which is independent of temperature, and *T. quadrispina*, which is not significantly correlated with either moisture or temperature. As these factors are themselves negatively correlated, however, their effects cancel each other out, and

population fluctuations cannot with certainty be attributed to either. The populations of both species of *Onychiurus* show winter maxima. The effect of freezing and flooding on the populations is also discussed.

6. The most appropriate standard of reference of the population density is discussed, and the population is expressed in terms of volume of soil, though it is recognized that it would be better expressed in terms of pore-space. The peak density of Onychiuridae corresponded to one animal to 8 c.c. of soil.

7. In every case the species were found to have widely differing properties, and the reactions of one species, or of the group Onychiuridae, were no guide to the reactions of the other species.

8. In Appendix 2 a convenient type of soil sampler is described; there is also a discussion of the advantages of the Ladell apparatus on p. 327.

APPENDIX 1. CENSUS COUNTS

Samples taken in the Pond Field at the Biological Field Station, Slough, between April 1936 *and October* 1937

α, 0–4·5 in. (0–11·4 cm.). γ, 9–13·5 in. (22·9–34·3 cm.).
β, 4·5–9 in. (11·4–22·9 cm.). δ, 13·5–16 in. (34·3–40·6 cm.).

Onychiurus armatus

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	14	10	—	—	13	7	—	—	2	4	—	—
18 May 1936	6	9	—	—	19	7	—	—	6	15	—	—
28 May 1936	9	15	—	—	11	13	—	—	23	20	—	—
16 June 1936	9	21	—	—	38	24	—	—	63	57	—	—
30 June 1936												
14 July 1936	30	16	8	—	45	25	9	—	72	51	24	—
28 July 1936	44	6	—	—	22	16	—	—	11	16	—	—
27 Aug. 1936	33	25	9	—	18	19	7	—	31	36	2	—
16 Sept. 1936	30	20	11	—	48	17	10	—	74	87	24	—
15 Oct. 1936	48	29	21	—	95	47	3	—	47	27	10	2
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	40	27	10	—	72	14	8	0	250	46	8	—
13 Jan. 1937	35	7	5	1	37	2	0	—	51	14	3	—
10 Feb. 1937	52	13	5	—	60	4	1	—	111	40	6	—
10 Mar. 1937	99	21	5	—	21	2	1	—	183	25	18	—
7 Apr. 1937	78	20	8	—	6	3	1	—	35	8	0	—
5 May 1937	35	8	14	—	33	3	2	—	108	46	23	—
9 June 1937	53	14	19	—	46	8	6	—	88	42	34	—
7 July 1937	108	73	43	—	27	12	6	—	72	41	23	—
27 July 1937	18	29	51	—	69	50	15	—	118	72	12	—
7 Sept. 1937	51	34	14	—	55	40	13	—	41	25	10	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	20	15	6	—	60	16	8	—	25	16	8	—

Onychiurus ambulans

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	24	41	—	—	4	8	—	—	15	11	—	—
18 May 1936	13	28	—	—	11	12	—	—	4	59	—	—
28 May 1936	5	34	—	—	5	18	—	—	4	20	—	—
16 June 1936	13	56	—	—	23	32	—	—	15	6	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	63	50	31	—	4	23	11	—	64	89	41	—
28 July 1936	222	17	—	—	19	48	—	—	56	91	—	—
27 Aug. 1936	99	62	34	—	52	40	16	—	49	37	13	—
16 Sept. 1936	148	93	78	—	30	26	19	—	21	26	31	—
15 Oct. 1936	131	62	46	—	32	28	9	—	142	84	63	17
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	103	152	75	—	28	24	15	1	53	65	28	—
13 Jan. 1937	226	268	118	5	15	13	6	—	95	165	91	—
10 Feb. 1937	198	113	119	—	20	55	55	—	47	62	54	—
10 Mar. 1937	156	124	65	—	32	24	12	—	49	78	30	—
7 Apr. 1937	157	126	137	—	22	32	14	—	273	207	149	—
5 May 1937	188	132	97	—	31	12	2	—	2	1	2	—
9 June 1937	74	101	56	—	32	30	18	—	41	54	52	—
7 July 1937	97	145	137	—	11	27	17	—	14	11	10	—
27 July 1937	9	40	60	—	11	21	16	—	23	63	15	—
7 Sept. 1937	30	38	26	—	14	33	7	—	18	29	7	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	169	213	104	—	71	43	43	—	48	59	16	—

Tullbergia quadrispina

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	36	35	—	—	11	22	—	—	5	5	—	—
18 May 1936	15	19	—	—	38	45	—	—	10	21	—	—
28 May 1936	36	101	—	—	22	52	—	—	13	11	—	—
16 June 1936	9	26	—	—	33	39	—	—	25	7	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	2	15	6	—	1	13	13	—	16	19	22	—
28 July 1936	35	7	—	—	11	27	—	—	5	21	—	—
27 Aug. 1936	15	21	9	—	11	20	10	—	9	22	3	—
16 Sept. 1936	43	53	62	—	38	28	22	—	10	18	10	—
15 Oct. 1936	21	20	36	—	22	14	12	—	24	31	24	10
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	32	24	18	—	36	23	93	28	32	16	5	—
13 Jan. 1937	13	11	8	0	44	21	19	—	33	26	18	—
10 Feb. 1937	15	21	33	—	44	81	77	—	24	17	12	—
10 Mar. 1937	51	54	49	—	20	29	30	—	17	27	27	—
7 Apr. 1937	22	23	15	—	16	20	15	—	17	29	29	—
5 May 1937	59	72	81	—	77	29	21	—	11	11	4	—
9 June 1937	9	12	5	—	22	47	6	—	19	30	14	—
7 July 1937	18	16	27	—	6	31	14	—	10	25	14	—
27 July 1937	3	7	10	—	17	65	30	—	6	15	1	—
7 Sept. 1937	4	6	4	—	15	45	13	—	19	14	17	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	16	19	30	—	67	50	54	—	16	13	15	—

Tullbergia krausbaueri

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	8	6	—	—	8	1	—	—	6	1	—	—
18 May 1936	24	1	—	—	24	12	—	—	16	21	—	—
28 May 1936	8	4	—	—	17	21	—	—	24	18	—	—
16 June 1936	8	15	—	—	23	47	—	—	29	23	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	34	26	6	—	88	52	13	—	42	15	9	—
28 July 1936	80	2	—	—	54	15	—	—	65	73	—	—
27 Aug. 1936	22	13	9	—	32	15	8	—	37	8	3	—
16 Sept. 1936	39	22	6	—	23	14	14	—	13	9	13	—
15 Oct. 1936	12	6	4	—	56	24	10	—	74	33	12	5
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	3	17	8	—	76	23	29	7	65	25	29	—
13 Jan. 1937	22	13	9	2	45	6	0	—	19	29	22	—
10 Feb. 1937	38	9	17	—	55	16	26	—	18	18	0	—
10 Mar. 1937	45	12	9	—	44	13	1	—	20	10	3	—
7 Apr. 1937	15	27	11	—	28	18	7	—	87	72	36	—
5 May 1937	27	15	4	—	29	3	6	—	20	7	0	—
9 June 1937	44	10	2	—	18	18	0	—	78	43	13	—
7 July 1937	13	5	2	—	24	5	2	—	8	4	1	—
27 July 1937	6	2	7	—	23	10	4	—	15	8	0	—
7 Sept. 1937	29	4	2	—	28	13	3	—	27	5	3	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	30	18	6	—	80	31	12	—	65	30	11	—

Onychiuridae (four species)

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	82	92	—	—	36	38	—	—	30	21	—	—
18 May 1936	60	57	—	—	93	76	—	—	36	116	—	—
28 May 1936	58	154	—	—	55	104	—	—	64	69	—	—
16 June 1936	39	118	—	—	117	142	—	—	132	93	—	—
30 June 1936	—	—	—	—	—	—	—	—	—	—	—	—
14 July 1936	129	107	51	—	138	113	46	—	194	174	96	—
28 July 1936	381	32	—	—	106	106	—	—	137	201	—	—
27 Aug. 1936	169	121	71	—	113	94	41	—	126	103	21	—
16 Sept. 1936	260	188	157	—	139	85	65	—	118	140	78	—
15 Oct. 1936	212	117	107	—	205	113	34	—	287	175	109	34
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	178	220	111	—	212	84	145	38	400	152	70	—
13 Jan. 1937	296	299	140	10	141	42	25	—	198	234	134	—
10 Feb. 1937	303	156	174	—	179	156	159	—	200	137	72	—
10 Mar. 1937	351	211	128	—	117	68	44	—	269	140	78	—
7 Apr. 1937	272	196	171	—	72	73	37	—	412	316	214	—
5 May 1937	309	227	196	—	170	47	31	—	141	65	29	—
9 June 1937	180	139	82	—	118	63	30	—	226	169	113	—
7 July 1937	236	239	209	—	68	75	39	—	94	81	48	—
27 July 1937	36	78	128	—	120	146	65	—	162	158	28	—
7 Sept. 1937	114	82	46	—	112	131	36	—	105	80	37	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	235	265	146	—	278	140	117	—	154	118	50	—

Moisture %

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	56·14	44·72	—	—	57·26	49·08	—	—	42·47	49·82	—	—
18 May 1936	42·98	42·22	—	—	37·89	39·17	—	—	43·87	46·95	—	—
28 May 1936	33·40	38·12	—	—	32·65	35·31	—	—	35·81	37·85	—	—
16 June 1936	48·40	41·39	—	—	46·12	41·40	—	—	43·00	43·52	—	—
30 June 1936	39·60	35·99	38·47	—	34·54	35·25	42·56	—	42·91	40·75	41·34	—
14 July 1936	62·52	42·65	28·70	—	51·30	37·44	39·45	—	56·06	49·27	46·51	—
23 July 1936	56·23	39·33	—	—	49·18	35·28	—	—	43·92	38·92	—	—
27 Aug. 1936	34·08	32·18	33·51	—	29·68	36·90	43·61	—	32·84	27·08	46·05	—
16 Sept. 1936	51·92	38·75	40·09	—	40·79	35·44	44·59	—	41·25	42·41	48·09	—
15 Oct. 1936	50·37	43·77	41·89	—	38·09	37·84	40·21	—	46·58	38·78	48·73	44·75
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	67·54	52·30	51·24	—	55·82	43·05	50·30	48·53	63·08	51·62	56·49	—
13 Jan. 1937	67·98	47·56	54·24	52·36	53·67	39·72	50·47	—	65·66	53·55	52·71	—
10 Feb. 1937	71·09	56·15	66·37	—	72·85	54·28	58·01	—	71·69	62·22	64·77	—
10 Mar. 1937	82·41	59·57	58·20	—	68·10	53·65	55·47	—	138·5	61·25	61·56	—
7 Apr. 1937	65·63	52·44	54·61	—	64·15	52·20	55·65	—	64·01	42·64	55·07	—
5 May 1937	70·25	46·23	49·33	—	50·59	40·34	48·35	—	70·52	56·69	54·59	—
9 June 1937	47·53	38·20	46·59	—	42·01	40·84	47·62	—	48·14	43·73	47·65	—
7 July 1937	42·51	39·93	41·72	—	38·02	42·94	46·55	—	44·30	43·18	47·19	—
27 July 1937	34·80	33·67	46·18	—	39·66	30·95	40·82	—	40·20	42·03	50·99	—
7 Sept. 1937	30·51	29·20	38·41	—	26·57	28·94	37·18	—	30·08	33·67	43·18	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937	37·43	34·98	42·98	—	29·71	30·31	41·30	—	40·37	38·23	46·98	—

Ignition loss %

	SW				NC				EC			
	α	β	γ	δ	α	β	γ	δ	α	β	γ	δ
20 Apr. 1936	—	—	—	—	—	—	—	—	—	—	—	—
5 May 1936	15·81	11·27	—	—	14·85	11·81	—	—	15·08	11·73	—	—
18 May 1936	14·27	11·13	—	—	12·76	10·17	—	—	14·34	10·86	—	—
28 May 1936	14·32	11·09	—	—	15·09	9·88	—	—	14·10	11·16	—	—
16 June 1936	14·37	10·67	—	—	13·64	10·89	—	—	12·72	10·22	—	—
30 June 1936	13·59	10·93	9·79	—	14·25	10·85	9·86	—	15·21	12·26	9·54	—
14 July 1936	13·46	10·77	10·72	—	14·51	11·31	10·70	—	13·86	10·84	10·25	—
28 July 1936	—	—	—	—	—	—	—	—	—	—	—	—
27 Aug. 1936	13·85	10·64	9·01	—	13·39	10·57	9·88	—	12·54	9·58	10·35	—
16 Sept. 1936	13·31	10·92	9·49	—	14·30	10·36	9·83	—	13·22	11·46	9·39	—
15 Oct. 1936	12·48	10·40	8·86	—	13·20	11·37	10·17	—	14·78	9·98	10·11	8·85
11 Nov. 1936	—	—	—	—	—	—	—	—	—	—	—	—
10 Dec. 1936	—	—	—	—	—	—	—	—	—	—	—	—
13 Jan. 1937	—	—	—	8·298	—	—	—	—	—	—	—	—
10 Feb. 1937				—	—	—	—	—	—	—	—	—
10 Mar. 1937				—	—	—	—	—	—	—	—	—
7 Apr. 1937	13·20	10·86	9·93	—	13·13	10·98	10·05	—	14·33	10·39	11·40	—
5 May 1937	16·59	9·97	8·92	—	14·23	9·20	9·38	—	15·30	11·44	9·88	—
9 June 1937	13·96	10·68	9·51	—	13·93	9·47	9·33	—	14·28	10·99	8·86	—
7 July 1937	13·91	10·89	9·71	—	13·78	10·77	10·21	—	14·02	11·59	9·73	—
27 July 1937	—	—	—	—	—	—	—	—	—	—	—	—
7 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
20 Sept. 1937	—	—	—	—	—	—	—	—	—	—	—	—
16 Oct. 1937				—	—		—	—	—	—	—	—

Onychiurus armatus

Totals for depths and occasions

	α	β	γ	δ	Total to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	46
5 May 1936	29	21	—	—	50
18 May 1936	31	31		—	62
28 May 1936	43	48		—	91
16 June 1936	110	102			212
14 July 1936	147	92	41		239
28 July 1936	77	38	—	—	115
27 Aug. 1936	82	80	18		162
16 Sept. 1936	152	124	45	—	276
15 Oct. 1936	192	103	34	6	295
11 Nov. 1936	—	—	—	—	213
10 Dec. 1936	362	87	26	0	449
13 Jan. 1937	123	23	14	3	146
10 Feb. 1937	223	57	12	—	280
10 Mar. 1937	303	69	24	—	372
7 Apr. 1937	119	31	9	—	150
5 May 1937	176	57	39	—	233
9 June 1937	187	66	59	—	253
7 July 1937	207	126	72	—	333
27 July 1937	205	151	78	—	356
7 Sept. 1937	147	99	37	—	246
20 Sept. 1937	—	—	—	—	203
16 Oct. 1937	105	47	22	—	152

Onychiurus ambulans

Totals for depths and occasions (see Figs. 2, 3 and 4)

	α	β	γ	δ	Total to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	65
5 May 1936	43	60	—	—	103
18 May 1936	28	99	—	—	127
28 May 1936	14	72		—	86
16 June 1936	51	94		—	145
14 July 1936	131	162	83	—	293
28 July 1936	297	156	—	—	453
27 Aug. 1936	200	139	63	—	339
16 Sept. 1936	199	145	128	—	344
15 Oct. 1936	305	174	118	51	479
11 Nov. 1936		—	—	—	481
10 Dec. 1936	184	241	118	3	425
13 Jan. 1937	336	446	209	15	782
10 Feb. 1937	265	230	228	—	495
10 Mar. 1937	237	258	107	—	495
7 Apr. 1937	452	365	300		817
5 May 1937	221	145	101		366
9 June 1937	147	185	126	—	332
7 July 1937	112	183	164		295
27 July 1937	43	124	91	—	167
7 Sept. 1937	62	97	40	—	159
20 Sept. 1937	—	—	—		324
16 Oct. 1937	288	315	163	—	603

Tullbergia quadrispina

Totals for depths and occasions

	α	β	γ	δ	Totals to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	54
5 May 1936	52	62	—	—	114
18 May 1936	63	85	—	—	148
28 May 1936	71	164	—	—	235
16 June 1936	67	72	—	—	139
14 July 1936	19	47	28	—	66
28 July 1936	51	55	—	—	106
27 Aug. 1936	35	63	22	—	98
16 Sept. 1936	91	99	94	—	190
15 Oct. 1936	67	65	72	30	132
11 Nov. 1936	—	—	—	—	190
10 Dec. 1936	100	63	116	84	163
13 Jan. 1937	90	58	45	0	148
10 Feb. 1937	83	119	122	—	202
10 Mar. 1937	88	130	106	—	198
7 Apr. 1937	55	72	59	—	127
5 May 1937	147	112	106	—	259
9 June 1937	50	67	25	—	117
7 July 1937	34	72	55	—	106
27 July 1937	26	87	41	—	113
7 Sept. 1937	38	65	34	—	103
20 Sept. 1937	—	—	—	—	147
16 Oct. 1937	99	82	99	—	181

Tullbergia krausbaueri

Totals for depths and occasions

	α	β	γ	δ	Totals to 9 in. (α + β)
20 Apr. 1936	—	—	—	—	30
5 May 1936	24	8	—	—	32
18 May 1936	64	34	—	—	98
28 May 1936	49	43	—	—	92
16 June 1936	60	85	—	—	145
14 July 1936	164	93	35	—	257
28 July 1936	199	90	—	—	289
27 Aug. 1936	91	36	20	—	127
16 Sept. 1936	75	45	33	—	120
15 Oct. 1936	142	63	26	15	205
11 Nov. 1936	—	—	—	—	242
10 Dec. 1936	144	65	66	21	209
13 Jan. 1937	86	48	31	8	134
10 Feb. 1937	111	43	43	—	154
10 Mar. 1937	109	79	13	—	188
7 Apr. 1937	130	117	54	—	247
5 May 1937	76	25	10	—	101
9 June 1937	140	53	15	—	193
7 July 1937	45	14	5	—	59
27 July 1937	44	20	11	—	64
7 Sept. 1937	84	32	8	—	116
20 Sept. 1937	—	—	—	—	158
16 Oct. 1937	175	99	29	—	274

Totals for occasions, to 9 in. ($\alpha + \beta$)

	Onychiuridae	"Other Collembola"
20 Apr. 1936	195	81
5 May 1936	299	81
18 May 1936	435	373
28 May 1936	502	264
16 June 1936	641	291
14 July 1936	855	512
28 July 1936	963	505
27 Aug. 1936	726	610
16 Sept. 1936	930	338
15 Oct. 1936	1109	576
11 Nov. 1936	1126	212
10 Dec. 1936	1252	411
13 Jan. 1937	1210	193
10 Feb. 1937	1131	411
10 Mar. 1937	1200	255
7 Apr. 1937	1341	278
5 May 1937	959	239
9 June 1937	895	334
7 July 1937	793	410
27 July 1937	700	494
7 Sept. 1937	624	556
20 Sept. 1937	832	338
16 Oct. 1937	1190	684

Moisture

Means for depths and occasions

	α	β	γ	δ	Mean to 9 in. ($\alpha + \beta$)
20 Apr. 1936	—	—	—	—	52·03
5 May 1936	53·96	47·82	—	—	50·92
18 May 1936	41·58	42·78	—	—	42·18
28 May 1936	32·79	36·44	—	—	35·19
16 June 1936	45·51	41·88	—	—	43·70
14 July 1936	56·63	43·12	42·98	—	49·88
28 July 1936	49·78	37·84	—	—	43·81
27 Aug. 1936	32·20	32·05	41·06	—	32·13
16 Sept. 1936	44·65	38·91	44·26	—	41·75
15 Oct. 1936	45·01	40·13	43·61	44·75	42·57
11 Nov. 1936	—	—	—	—	52·16
10 Dec. 1936	62·15	48·99	52·68	48·53	55·57
13 Jan. 1937	62·44	49·94	52·47	52·36	54·69
10 Feb. 1937	71·88	57·55	63·05	—	64·72
10 Mar. 1937	96·34	58·16	58·41	—	77·25
7 Apr. 1937	64·60	49·09	55·11	—	56·85
5 May 1937	63·79	47·75	50·76	—	55·77
9 June 1937	45·89	40·92	47·29	—	43·40
7 July 1937	41·61	42·02	45·15	—	41·82
27 July 1937	35·55	35·55	46·00	—	35·55
7 Sept. 1937	29·05	30·60	39·59	—	29·83
20 Sept. 1937	—	—	—	—	39·53
16 Oct. 1937	35·84	44·51	43·75	—	40·17

Ignition loss

Means for depth and occasions

	α	β	γ	δ	Mean to 9 in. $(\alpha+\beta)$
20 Apr. 1936	—	—	—	—	12·43
5 May 1936	15·25	11·60	—	—	13·56
18 May 1936	13·80	10·70	—	—	12·25
28 May 1936	14·50	10·70	—	—	12·68
16 June 1936	13·58	10·59	—	—	12·08
14 July 1936	13·94	10·97	10·57	—	12·46
28 July 1936	—	—	—	—	—
27 Aug. 1936	13·25	10·26	9·75	—	11·77
16 Sept. 1936	13·61	10·91	9·57	—	12·26
15 Oct. 1936	13·49	10·58	9·71	8·45	12·04
11 Nov. 1936	—	—	—	—	12·67
10 Dec. 1936	—	—	—	—	—
13 Jan. 1937	—	—	—	8·30	—
10 Feb. 1937	—	—	—	—	—
10 Mar. 1937	—	—	—	—	—
7 Apr. 1937	13·55	10·78	10·46	—	12·15
5 May 1937	15·37	10·21	9·40	—	12·79
9 June 1937	14·06	10·38	9·23	—	12·22
7 July 1937	13·90	11·08	9·88	—	12·49
27 July 1937	—	—	—	—	—
7 Sept. 1937	—	—	—	—	—
20 Sept. 1937	—	—	—	—	12·06
16 Oct. 1937	—	—	—	—	—

Appendix 2. A simple soil sampler

Work on the soil may necessitate taking in large numbers samples much larger than those of the soil chemist. It is not easy to take a large sample accurately. The custom has been either to cut the sample from a large block which has been dug with a spade and brought into the laboratory (Ford, 1935) or to drive a number of iron plates into the ground to form a box from which the soil is scooped (Morris, 1922; Baweja, 1937). Both methods are laborious, and the first makes an unnecessarily big hole in the ground.

Fig. 5.

The tool illustrated takes a quick accurate sample of 8 sq. in. (51·6 sq. cm.). A sample of 8 sq. in. by 13·5 in. (34·3 cm.) deep weighs about 5 lb. (2·3 kg.). It has been successful in a heavy clay soil without many stones. It is simply a sharpened galvanized iron pipe of internal diameter 3·2 in. (8·1 cm.), this being a standard size. A half-inch slot at the lower end facilitates removal of the soil. The cutting edge is case-hardened on the inside, so that wear is differential and the edge keeps sharp. If this is not done, frequent sharpening is necessary. Holes bored through the big pipe take 1 in. pipes for the handle and foot-rail. When using it the operator stands on the foot-rail with the handle in his hands, and by wriggling rotates the sampler backwards and forwards. In this way the pipe is quickly sunk into the ground. A certain knack is required to do this, but it is very soon acquired. On withdrawing the sampler, the soil is removed by introducing a suitable instrument through the slot.

Where samples from different depths are required, the sampler is sunk to the depth of the first layer, removed and emptied, then replaced in the same hole and sunk to the

next layer, and so on. Routine samples were taken to 13·5 in. (34·3 cm.) and occasional samples to 16 in. (40·6 cm.). Deeper samples could no doubt be taken in lighter soils. For references see Baweja (1939), Ford (1935), Morris (1922).

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SPECIAL REVIEW

RECENT RUSSIAN WORK ON COMMUNITY ECOLOGY

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PART 1. GENERAL REVIEW

1. Introduction

The purpose of this review is to offer to the student of ecology an introduction to the work which has been done in the field of community ecology in the U.S.S.R. The apparent difficulty of the language has caused an evident tendency to ignore much of the important and valuable work which has been done by Russians since the War. This is particularly to be wondered at since many of the papers have abstracts in English, German or French.

It is desirable to indicate what is meant here by community ecology. The term is not used in the restricted sense of studies of whole communities only, but to cover various aspects of synecology: the dynamics, structure, organization and functioning of biotic communities or parts of them, the interactions of the constituent species among themselves and with the habitat, and methods for their investigation. Owing to the enormously large literature involved, and for practical reasons, the plant aspect has only been discussed in connexion with the general development of ecological concepts; and the references, while often containing information about the relation of animals to plants, largely deal with animal ecology. The line drawn between synecology

[1] After the author had left England for the United States in 1938, a considerable amount of editing work was done by Mr Charles Elton, who with the assistance of Miss N. Waloff, verified from original sources most of the references given at the end of the paper. The author is entirely responsible for the paper generally, for the translations given in the text, and for those references (marked *) which could not be checked. Ed.

and autecology cannot be an exact one, and many of the papers included may be considered rather beyond the defined limits of the review, while others may have been omitted or overlooked. The inevitability of this requires no apology. Regarding the earlier time limits of this review it will immediately be recognized that the development of the community concept has everywhere been largely post-war (Shelford's *Animal Communities in Temperate America* appeared in 1913, and the work of Adams, Hankinson and Vestal *circa* 1915), and that community studies in pre-war Russia would therefore of necessity be restricted to botanical studies. The "ecological method" in the study of animals was advancing up to and through the War period; but since it has been necessary to review the biotic community work of synecology, this autecological work will have to be passed over briefly. The review, therefore, is restricted to the period since the War and up to the end of 1937. Any such review will be out of date before it is published, but it is hoped that it will at least encourage an interest in the Russian work which is being done to-day and that it may serve as a rough, though admittedly incomplete guide to the literature of the past two decades.

2. Ecology before 1919

As has been stated above, early ecological studies were largely botanical. Perhaps the earliest ecological studies were those made by foreign botanists travelling through Russia (notably von Blasius, Schrenk and Trautvetter) in the 1840's. Again in the eighties a number of accounts of Russian plant geography appeared, many in foreign languages by non-Russian authors. A bibliography of the work of this period may be found in Kuznetzov's "Uebersichten der über Russland erscheinen phytogeographischen Arbeiten" (1898, etc.). There is also an account by Batalin (1881): "Aperçu des travaux russes sur la géographie des plantes de 1875 1880." The *Humboldt Centarschrift* (Gesellschaft für Erdkunde, Berlin), 1899, should also be consulted in this connexion. It is noteworthy that these earlier studies, done before the full impact of the Darwinian influence on scientific research had occurred, had little to do with the later revival of ecology as we know it to-day. However, plant ecology developed towards the turn of the century, as is indicated by the publication of the Russian translation of Warming's *Plantesamfund* (*Oecology of plants*) in 1901, eight years before its translation into English. Other indications of its development were the surveys—largely ecological—which were conducted by Fedchenko and published by the Ministry of Agriculture, of the sparsely populated areas of Siberia and the Far East, undertaken with the idea of organizing planned emigration of peasants from the overcrowded areas of European Russia. Plant ecologists of the pre-War period who should be mentioned are, in addition to Fedchenko: Alekhin, Elenkin, Il'inskii, Korzhinskii, Kuznetzov, Morozov, Pachosskii, Ramenskii, Shenikov, and Sukachev.[1]

[1] For a comment on the method of transliteration of Russian names, see p. 366.

Animal ecology prior to 1919 was, strictly speaking, autecology (as was largely the case elsewhere). Notable exceptions were N. A. Severtzov's two publications, *Periodic phenomena in the life of the mammals, birds and reptiles of the Voronezh District, based on observations during* 1844–53 (1855), and *The vertical and horizontal distribution of the animals of Turkestan* (1879). Some beginning of ecological observations had been made previously by Nordmann (1833) in south Russia, by Baer (1839) on Novaya Zemlya, and by Middendorff (1875) in northern and eastern Siberia. In the works of Eversmann (1840) for the Aral-Caspian basin, of Menetrié (1850?) for the Caucasian mountain altitudinal zones, and of Chernai (1853) for the Kharkov Government, we find lists of animals to be found in various habitats or stations (statio). Chernai and Severtzov were both influenced in their studies by the lectures (published in 1852) of Rule, who emphasized the need for studying associated plants and animals in relation to their surroundings. Apparently Rule's recommendations had but little further effect until very recently in the encouragement of ecological study. The early "ecological" studies were to some extent zoogeographical, but Russian zoogeography had its modern beginning with the works of Menzbir (*Ornithological geography of European Russia*, 1882; *Zoogeographical atlas*, 1912). It is interesting to note that Kobelt's *Die Verbreitung der Tierwelt* was translated into Russian in 1903, and Scharff's *European animals* in 1918. Hydrobiology had for some time been studied fairly intensively (see Zernov, 1921): the many lakes of the glaciated portion of Russia as well as the larger southern ones offered many opportunities for this type of investigation; the names of Deryugin and Zernov should be mentioned in this connexion. The work was both faunistic and limnological, probably being influenced to some extent by the German research in fresh-water biology which was done during the latter portion of the nineteenth century.

3. Post-war advances in ecology

The recognition of the biotic community concept in Russia was apparently first made in hydrobiology. Its application to terrestrial studies was pointed out by Alpatov (1923) in a paper reviewing the American work of Shelford and Adams and their associates and giving a general account of the aims and methods of ecology. Shortly after this date, Alpatov went to America as a research fellow of the International Education Board and worked for several years on *Drosophila* at Johns Hopkins University. His association at Johns Hopkins with Pearl is reflected in one of Alpatov's students, Gause. In 1923 Dogel began the publication of a series of studies on the fauna of individual plants and of vegetation strata, which was supplemented by Vladimirskii and other associates. In 1924 Beklemishev began the direction of a series of studies at the Biological Station of the University of Perm, and a number of interesting publications on community ecology by him and his students began

to appear. Kashkarov had been influential in instigating and encouraging ecological work, and in 1928 visited a number of institutions in America; on his return he initiated the *Journal of Ecology and Biocenology*, which was later reorganized to appear as a yearly publication, *Problems of Ecology and Biocenology*. The extension of community methods about 1929–30 to the acute locust problem, which was already advanced in the methods of autecology, contributed to the rapid advance of synecology (or "biocenology", as it is termed in Russia and elsewhere on the Continent); names which are especially important in this connexion are Bei-Bienko, Ivanov, Nefedov, Predtechenskii, Rubtzov, and Vinokurov, in addition to many others. While there is no adequate review of the extensive work on locust ecology, the bibliographies in the works of Uvarov (*Locusts and Grasshoppers*, 1931) and Predtechenskii *et al.* (1935) are fairly extensive and give an introduction to the copious literature on the subject.

Kashkarov gives the following account (translated from Kashkarov, 1937*b*, pp. 214–15) of the growth of Russian ecology:

> The extent of ecology in the U.S.S.R. before 1930 may be seen in the *Proceedings* of the Congresses of Zoologists. Already in the first Congress, held in December 1922, ecology had an official place in the ranks with systematics and zoogeography, which it had not had in the previous Congresses of Naturalists. Of the 29 papers in the section of Systematics, Ecology and Zoogeography, seven were ecological. Co-ordinated with this section was the section on Hydrobiology, where there were about 10 papers of an ecological character. In the second Congress (May 1925), of 46 papers in the section of Systematics, Ecology and Zoogeography, 12 were ecological, a series of ecological papers were presented in the section on Hydrobiology, and, finally, in this congress there were seven sections dealing with applied zoology, some of their papers having an ecological character. The third Congress (December 1927) had ecological papers of a general character read in the plenary session (by Beklemishev, Kashkarov, Dembovskii and Pavlovskii), and a series of papers on ecology in the section of systematics, ecology and zoogeography. Even a greater number of ecological papers were read in the fourth congress (May 1930), both in the general assembly and in the usual section. Also, there was passed a resolution on ecological topics, regarding the indispensability of the ecological study of economic animals and the necessity of work on the methods of collecting quantitative data, etc.

In addition to the four meetings of the All-Union Congresses of Zoologists mentioned by Kashkarov, several other assemblies should be mentioned, namely, the All-Ukrainian Zoological Conference held in 1931,[1] Botanical Congresses held in 1926 and 1928, and a Hydrobiological Congress in 1930. There was an Anti-Plague Conference in 1927, and there have been many others on various topical subjects (e.g. on specific injurious rodents, etc.) which have been held from time to time. Several discussion groups have been organized at Leningrad, Moscow and Voronezh; the two discussions reported in *Soviet Botany* (1934, No. 3 and No. 5) were held in the Leningrad Botanical Institute under the auspices of Keller and Kashkarov; both botanists and

[1] J. Cycle Bio-Zoologigue, 1–2: 105–20. *Ug.*

zoologists were represented. The meetings of the Ecological Committee of the Leningrad University Society of Naturalists are reported in *Problems of Ecology and Biocenology.*

Ecology has begun to be taught in the universities: in 1924 there was begun a course in ecology at the Middle Asiatic State University (Tashkent) by Prof. D. N. Kashkarov, in 1925 by I. Strel'nikov in the Leningrad State University. In the University of Moscow there is a course by Prof. Alpatov, in Smolensk and later at Kharkov by Prof. V. Stanchinskii, in Voronezh by Dotzent Konakov, etc. Besides courses in general zoology in Leningrad there is also a course in experimental ecology. There is also given in a number of universities a course in the ecology of plants (by Korovin in Tashkent, Poplavskaya in Leningrad, etc.). Work is not organized wholly by courses; in a number of universities and institutes there have been organized laboratories of ecology: in the Leningrad State University, in Moscow State University (the first Russian ecological laboratory, founded in 1931); in the Peterhof Biological Institute of the Leningrad State University there is organized a laboratory of experimental ecology; also, there are the laboratories of the Leshaft Institute and the laboratory of ecology organized by the Zoological Institute of the Academy of Sciences, the All-Union Institute of Plant Protection, the Institute of Hybridization and Steppe Acclimatization in Ascanya Nova, the Scientific Research Institute in Kharkov, the Institute of Zoology and Biology of the Ukrainian Academy of Sciences, the Middle Asiatic University, the Uzbekistan Institute of Experimental Medicine, etc. (Translated from Kashkarov, *loc. cit.*)

A note should be added as to the general method of carrying out investigations. The development here may be roughly divided into two periods of a decade each. During the first period many expeditions were sent throughout the country collecting data and material. "Much material was collected by these expeditions, in post-revolutionary times the network of their paths covering even the most remote and inaccessible parts of the country." (Translated from Formozov, 1937*c*, p. 928.) Men important in the directing of these expeditions and the processing of material after their return were Ognev, Vinogradov, Geptner and Bobrinskii, among many others.[1]

These expeditions sometimes gave valuable material on the geography but only partly on the ecology of mammals. In the collecting parties there are now included numerous hunters and amateur naturalists who often are able to kill masses of material for this or that problem. The second decade of investigation was the period characterized by the rise of a number of biological stations and the transition from the expedition as a method of work to one of utilizing stations....The zonal organization of stations for the investigation of the ecology of economic animals is an unbroken complex network of state Preserves of Natural Conditions....The introduction of biological stations in preserved areas, the observation from various points by the Administration of the North Sea Passage and the filial organizations of the U.S.S.R. Academy of Sciences have made it possible in recent years for Soviet ecology to determine rapidly a series of important theoretical and practical problems. (Translated from Formozov, *loc. cit.*)

[1] The more recent expeditions which have been supervised and sent out by the Zoological Institute of the Academy of Sciences are discussed by Pavlovskii, 1937.

4. The organization of ecological research in the U.S.S.R.

The organization of science in the U.S.S.R. is entirely a part of the government organization and has its purposes defined in each five-year plan (*pyatiletka*). The government of the U.S.S.R., the All-Union Congress of the Soviets, does nearly all of its administration through the Central Executive Committee (TZIK). Scientific organizations in the several republics not included in the R.S.F.S.R. (e.g. the Turmen S.S.R., the Ukrainian S.S.R., the Armenian S.S.R., the various Caucasian republics, etc.) are, strictly speaking, not responsible to the TZIK, but inasmuch as all are, in the last analysis, responsible to the All-Union Congress, close co-operation and similar organization are carried out.

So far as ecological research is concerned, there are three essential bodies in the U.S.S.R. with which we are interested: the Academy of Agricultural Sciences, the Academy of Sciences and the Committee for Higher Technical Education, in addition to the organizations of the individual republics which will be mentioned later. The Lenin All-Union Academy of Agricultural Sciences (also sometimes called the Agrarian Institute; literally, in Russian, the "All-Union Academy of Agricultural Sciences named after Lenin") has as one of its institutes the Institute of Plant Protection (also sometimes called the Institute of Pest Control), VIZRa, where most of the ecological work of this Academy is done. The more recent work and the present problems being considered may be found discussed in an article by Rainey (1938). The Academy of Agricultural Sciences was, until 1935, a part of the late Communist Academy (before 1926 termed the Socialist Academy).

The All-Union Academy of Sciences of the U.S.S.R. has a long history, having been founded by Peter the Great in 1724–5. It maintained its essential organization of the pre-revolutionary period until about ten years after the revolution, when it was reorganized. There are 93 active members, only a small proportion of whom are party members; it also has about 68 honorary members and about 300 corresponding members. While various authorities give various compositions of the membership of the Academy, there being no doubt some changes from time to time, the following figures give a representative idea of the membership in, at least, 1935: Mathematics, 4; Physics, 8; Technics, 18; Chemistry, 10; Geology, 8; *Biology*, 13; History, 6; Social Economy, 6; European Languages and Literatures, 10; Orientology, 8; Philosophy, 2. The Academy is divided into three great departments, those of Sociology, Technics, and Natural and Mathematical Sciences. The latter department is divided into what are known as "associations" of sciences: the physico-mathematical association, the geological association, the chemical association, and the biological association. Included in the latter are the following institutes and laboratories, located either in Moscow or Leningrad: the Institute of Genetics, the Palaezoological Institute, the Physiological Institute, the Laboratory of

Microbiology, the Laboratory of Biochemistry and the Physiology of Plants, a similar laboratory for animals, the Institute for Forest Research, the Laboratory of Zoogeography, the Laboratory of Experimental Zoology and the Morphology of Animals, the Botanical Institute and the Zoological Institute; it is in the last four that most of the ecological work is done. Certain biological stations are also attached to the Academy of Sciences, e.g. the Sevastopol, Baikal and Khibin stations.

The Academy itself was officially transferred to Moscow in 1934, but there is still a branch ("filial") in Leningrad; other filial organizations may be found in various places throughout the U.S.S.R., e.g. in the Urals, Tajakstan, Azerbad, Kazakstan, Transcaucasia, Vladivostok, etc. (There are also Academies of Science in Ukraine and in White Russia.) Co-ordinated with these filials there are a number of "bases" which are used as more or less temporary stations for many expeditions, and which sometimes later may become permanent stations or filial organizations. Examples of these bases are those in Tajakstan, Kol'sk, and the polar bases. The filials usually have several institutes of biology, geology, chemistry, and the Far-Eastern Filial at Vladivostok has a fresh-water biological station, the Kedrovaya-Padi preserve, and a seismic station as well.

Certain other biological stations are under administrations other than the Academy of Sciences; for example, the Arctic Institute (formerly the Institute for the Scientific Exploration of the North) is under the direction of the Chief Administration of the North Sea Route, the Kossino Limnological Station is under the Moscow-Kazan Waterway Commission of the Hydrometeorological Administration, the Azov-Black Seas Scientific Fisheries Station and the State Oceanographic Institute (Moscow) are under the Department of Food Industry, and the Institutes for Microbiology and Epidemiology at Rostov-on-Don and Saratov are under the Public Health Department. Other stations are controlled by the Universities and Societies of Naturalists: the Peterhof Science Institute is run by the Leningrad State University; the Murman Biological Station (at Alexandrovsk) by the Leningrad Society of Naturalists; the Zvenigorod Hydrophysiological Station by the Zoological Institute of the University of Moscow; the Bolchevo station by the Society of Friends of Natural Science, Anthropology and Ethnology; the Kama Biological Station by Perm University; a bio-station by the Gorky (Nizhni-Novgorod) State University; and the Donetz Biological Station by Kharkov University. There is also a wide network of State Preserves, each usually having a station. Preserves which may be mentioned are the Chapli Steppe Preserve (under the Ukraine Academy) at Askanya Nova, the Crimean Preserve at Aluishita, the Azov-Sivash Preserve, the Caucasian and Astrakhan Preserves, the Volga-Kiev Preserve at Pensa, the Smolensk Forest Preserve, the Kedrovaya-Padi, Sikhote-Alin and Khibin Preserves in the Far East, the Izmailovsk Preserve near Moscow, the Lapland Preserve, the Naupzumsk, Tajakstan, Voronezh and Kursk

Preserves, in addition to many others which have not been so well studied. Other biological stations which should be mentioned are the Arnoldi Station at Novorossisk, the Borodin Station at Leningrad, the Volga-Kama Station, the Novosibirsk Station, the Kertch Limnological Station in the Crimea, the Karadagsk Station, and the Turkemhistan Zoological Station.

There are also several institutes of interest which have not yet been mentioned: the Tropical Institute (Moscow and Uzbekistan), the Subtropical Institute at Tashkent, the Pacific Institute of Fisheries and Oceanography at Vladivostok, the Zoological Gardens at Moscow and Novosibirsk, the Solovetzk nursery, the Nikitsk Botanical Gardens, etc., where ecological observations are made on animals and plants. Probably most important of all, however, are the ecological laboratories in the various institutes of zoology, biology and botany at the universities at Leningrad, Moscow, Perm, Voronezh, Tashkent, Kharkov, etc.

When plotted on a map of Russia, these stations, preserves, laboratories and institutes cover very well indeed the European part of the Union as well as "Middle Asia" and the Far East, although there appears at present to be a gap in the central portion of Siberia. The work done by these various institutes may be judged by the fact that a number of them issue their own publications to which references are made in the bibliography.

5. Concepts and theories

The Russian concepts of biotic community ecology are somewhat different from those of the Scandinavian and American schools of thought, although adherents to both these may be found. The precise meaning of the term "biocenology", together with the underlying ideas of the Russian ecologists, may perhaps best be conveyed by citations from the translated conclusions of several important papers dealing with the question. These are cited here because such important reviews of ecological thought as Phillips' in the *Journal of Ecology* (1931, 19: 1–24) have included no reference to the Russian concepts. Most of the citations below have been made by translation. It will be noted that the biotic concept had its origin in Russia in connexion with hydrobiological studies.

Filip'ev (1924): The term "biocenosis", introduced to science by Möbius (1877), is often met in the Russian hydrobiological literature into which it was introduced by Zernov in 1912, but various authors have employed it in very different senses. The purpose of this note is to propose an exact terminology which will be able to minimize confusion.

1. Facies: the lithological properties of the sea bottom. The organisms are able to inhabit the sea bottom, but it is only their inorganic parts which contribute to its formation.

2. Station: a part of the sea bottom which, due to similar physico-chemical conditions, bears similar faunas.

3. Biocenosis: the sum total of the constant population of a stratum, without taking into account the special relations of the organisms between themselves or to the substratum (i.e. the "animal community" of Petersen).

4. Association: a group of organisms united by conditions of existence, by plants, animals, or only by the substratum.

5. Ecological group: an assemblage of organisms with one ecological parallel: herbivores, planctonivores, leaping forms, swimmers.

Ecological analysis of the benthos may go in two directions: centrifugally—the physiological study of separate forms—and centripetally—a division into proposed groups. The second method reduces the complexity of the population of the sea and permits of an easier orientation.

The biocenosis has every right to be studied for itself, all the more since it is the only basis which conveys to us the significance of the organization of the sea. It is the only means of having this rich material contribute to the analysis of the great problem of the general economy of sea life.

Resvoi (1924): A biocenosis is a dynamic state of equilibrium maintaining a population-system, this equilibrium arising under given ecological conditions.

From Möbius's representations it is clear that the biocenosis is, above all, a versatile or dynamic state of equilibrium. In biology the presence of a "system of dynamic equilibrium" [bewegliche Gleichgewichtssystem] was first designated by Elenkin in 1921. The "ecological conditions" should be understood to mean the sum of the influences, both the conditions of outer existence and the element of the continuity of life or of organisms, which populate the habitat [Lebensraum] concerned. In short, all conditions which represent the environment of the given biocenosis. The habitat of the biocenosis—all parts of it, biologically speaking—must likewise be of equal or similar conditions. Such a habitat is meant by the designation "biotop" (Dahl, 1903–21), or "statio" [=station] (Vereshchagin, 1914; Filip'ev, 1923). Both designations are wholly identical in their meaning.

From the above it follows that the biocenosis is composed by the population of the biotop. Between the properties of a given habitat and its population (i.e., between a biotop and its biocenosis) a functional connexion is always present. For each environmental variation [Milieu-Veränderung] there will be a corresponding resultant in the population; each variation in the population (e.g. through the activity by man) must call for a corresponding result in the variation of the environment.

Only to a certain point is a biocenosis a self-sufficient and strongly contained system: the biocenotic relationships go beyond the boundary of the biocenosis, and the boundaries of a biocenosis in water depend on the articulation of these latter interrelationships.

Beklemishev (1931) ["The organism and the biocenosis"]: One of the most important questions of biocenology is the following: May the natural communities of organisms be considered as organic individuals or organisms and in what degree? It is wholly a mistake to implicate the criterion of individuality in the diagnosis of communities or, on the contrary, to eliminate it for *a priori* reasons. The question of individuality of each biological object must on each occasion be answered inductively. And it is necessary for us to be clear in each individual case what we mean by a "living individual", "organism", or "community" (Gesellschaft, biocenosis, etc.).

Organization is the chief criterion of an organism....If the conceived system possesses the criterion of having its living parts regulated so as to form a constant, we may then speak of an organism; it would be better to speak of a higher degree of organization, since most (or all) organisms are composed of parts each of which in their turn have an unquestioned individuality. And to understand the social structure of every organism we must prove the degree of individuality of each part itself, i.e. all valid regulatory mechanisms which are exhibited and which are maintained by the specific structure and the specific functions of the given part. Corporeal continuity is, on the other hand, not a necessary criterion of the organism, any more than the origin (through aggregation or differentiation).

The Biocenosis. Plant sociology is in possession of a great arsenal of concepts concerning the distinction between the different types of plant communities, and if the botanists are still far from agreement among themselves, there are certainly several concepts which are apparently generally acknowledged. Among the zoologists the Americans are using the botanical terminology most, and are correct in so doing. The Western Europeans and the Russian zoologists and hydrobiologists employ as a rule one single expression: the biocenosis. Their meaning of the biocenosis is thus the same as that of the early concept of the "plant association" of the 1910 Botanical Congress in Brussels, which expresses the meaning of the word biocenosis as it is generally used in the literature to-day, be it used in the abstract or concrete sense.

It appears to me that most definitions have not adequately described the content of the biocenosis concept. From Möbius up to Resvoi we find more and more concepts being introduced into the biocenosis concept, as if it were a strong storehouse of concepts. Our first task is to study the structure of the life covering the earth and to designate the natural constructive rankings. As logical outgrowths of this we shall study (1) the biocenotic units or cenoses and their interrelationships, and (2) the sociological significance within the cenoses (regulatory mechanisms, the functioning of the equilibrium, etc.). We will obtain, so to speak, an anatomical and histological analysis of the geomerid,[1] the life clothing the earth. We must state from which constructive unity and by what manner this covering of the earth is put together, and then investigate to which of these unities and in what degree the definitions of Möbius, Vereshchagin or Resvoi correspond.

Beklemishev criticizes the

artful partition of populations of organisms of every habitat [Standort] in a phytocenosis, and the superimposing of a higher taxonomic category of the Linnean system on it without meaning. "Life forms" and "basic forms" [Grundformen], not kingdom and class, should be applied to the biocenotic distribution of organisms." [The concepts of the continental plant sociologists (whose emphasis is upon small "synusia") are considered as insufficient to cope with biotic phenomena.] Among the organisms one can always find in similar layers and aspects of a cenosis animal species which live in neighbouring growths with the same plants and with different animals. A common view of plants and animals would complicate the present methods and concepts of plant sociology very much. The question of stratum existence of motile animals, for example, includes a difficulty which is wholly unknown to the phytosociologists. Periodic or unperiodic migrating animals complicate the question of the time aspects of communities. Larger animals often belong to the larger biocenotic units without having attachment with the smaller; for example, in the Kama lowlands the hare belongs to a known meadow complex and has no relation [Verbindung] with plant associations belonging thereto.... We must leave the "association concept" of the plant sociologists to them, and stand by the biocenosis concept of the zoologists....

That the biotic concepts of Beklemishev are not held by all Russian ecologists is indicated by the work of Sukachev (1918), a plant ecologist adhering to the ideas of the Swiss school of ecology:

A phytocenosis is the sum total of a given territory organized through the struggle for existence among the dominant plants with the conditions of the habitat [Standort], and characterized by the given mutual relations of the plants to one another as well as to their habitat.

A plant association or "phytocenosis type" is essentially uniform through the struggle for existence competition and corresponds to the habitat relations of organized phytocenoses.

[1] Expressed by K. D. Starinkievich, who designated the sum total of life as the highest biocenosis, as would be meant by terming the biosphere the highest biotop (Vernadskii, 1926).

Therefore it is accommodated equally throughout to the moisture requirements for existence, i.e. phytocenoses which have essentially similar species lists, structure, and composition of the distinguishing synusia of which they are constructed. External physiognomy and biological uniformity through a similar complex of communities enable the formulation of the influential factors of habitat conditions.

A practical view of the purposes of ecology is taken by Bukovskii (1935) who considers that the Americans place undue emphasis on the details of biotic succession and finds it a "fatalistic" phenomenon,[1] the Western Europeans place too much emphasis on structure [cf. the view of Beklemishev above], and the hydrobiologists too much upon the equilibrium and the balance of populations:

> The basic aim of biocenology is to study the laws that govern the dynamics of biocenoses and to regulate their quantitative and qualitative content, and, having obtained strictly scientific data, to produce the alterations in the composition of biocenoses that we find desirable.

Minin (1936): The station is a unit of the arena of life, characterized by a complex of edaphic, biotic and climatic factors, more or less separated from the neighbouring units of the same life-zone, and still more from those of different life-zones. [See comment of Shelford which follows.]

The term "biotop" must be looked upon as synonymous with the term "station"; it also is a division of the space of life. The term "habitat" is employed by most ecologists in the same sense. The term "habitat" must be related not to space but to species. The habitat is the complex of ecological conditions necessary for the evolution of the complete life-cycle of a species population. The habitat of a species can include many biotops (or stations) and in one biotop can be many habitats.

Veitzman (1936) cites the use of the term "constation" as including all of the "stations" occupied by an organism, but criticizes its being applied to all habitats occupied during the entire life-history of such migratory organisms as certain birds.

As a closing word in considering Russian ecological concepts, an observation of Shelford (1934) should be reiterated: the "life zones" described by Filip'ev (1929*b*), Kashkarov (1927)[2] and Kashkarov & Korovin (1931) are based on the natural vegetation regions and hence are not comparable to the so-called "life zones" of Merriam and others for North America which are based on temperature summation. The use of similar terms here is unfortunate.

6. Acknowledgements

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[1] There is no way of knowing how widely this view is held, but the scarcity of papers dealing with biotic succession may be pointed out; those of Plyater-Plokhotskii (1936) and Bei-Bienko (1936) are notable exceptions.

[2] ["An ecological study of the environments of Lake Sarg-Tshilek, North Ferghana."] Turkestan. *Rg.*

Moscow, and for his suggestions during the preparation of the manuscript; Prof. D. N. Kashkarov and Prof. A. N. Formozov for copies of several papers summarizing certain phases of Soviet ecological work; Prof. A. C. Hardy of University College, Hull, for information about certain Russian publications on oceanography; and Dr B. P. Uvarov for suggestions and criticisms. I am particularly indebted to Mr Charles Elton for the editorial work he has done on this paper (see footnote on p. 354), and to Miss N. Waloff who assisted him in checking references; also to Mr Elton for advice and for the use of the Russian publications in the Bureau of Animal Population. I also wish to thank the library staff of the Imperial Institute of Entomology and the British Museum (Natural History) for their assistance in making available many publications.

While I am indebted to all these people for various services, it should be pointed out that the opinions expressed in the text, unless indicated as quotations, are entirely my own, and for them I alone am responsible.

PART 2. SELECTED BIBLIOGRAPHY

7. Current bibliographies

As mentioned in the introduction to Part 1, any guide to current literature will be out of date before it is published. The most that can be done to remedy the situation, therefore, is to suggest the generally available means of keeping informed concerning the large amount of Russian ecological literature which is now being published. The bibliography in this Part includes a number of summaries of work on various subjects not included in this review; 1937 was a "peak year" for summaries of this type, it being the twentieth anniversary of the Revolution.

Other publications which help one to keep abreast of the current literature are the especially valuable *Miscellany* (or "*Abstracts of the Works of*") *the Scientific-Research Institute of Zoology of Moscow State University* (which contains summaries and bibliographies of the work done in its various departments); *Problems of Ecology and Biocenology* (which contains, in addition to many ecological papers, a "chronicle of ecological investigation in the U.S.S.R." and the proceedings of the Ecological Committee of the Leningrad University Society of Naturalists); the *Summary of the Scientific Research Work of the Institute of Plant Protection* (1935 edition being summarized in English in the *Rev. Appl. Ent.* A, 25: 137–60); and the *Bulletin of the Arctic Institute*[1] (which contains many notes and bibliographies of publications, both Russian and foreign, relating to investigations in the Northern Regions). A section entitled "Bibliographia hydrobiologica rossica" appeared in each number of the now extinct *Russkii Hydrobiologicheskii Zhurnal* (i.e. up to 1930), and included bibliographies in Russian and English French German on all papers dealing with Russian hydrobiology.

In addition to the above Russian publications, the following also frequently

[1] Now no longer issued, being partly replaced by *Sovetskaya Arktika*.

contain references to Russian ecological work: *Biological Abstracts*, the *Zoological Record*, the *Berichte über wissenschaftliche Biologie*, the *Review of Applied Entomology*, the *Tropical Diseases Bulletin*, and the *Journal of Mammalogy*.

Beginning with the 1936 publications, the Russian zoological literature is being collected by the Library of the Zoological Institute of the Moscow State University under the direction of Prof. V. V. Alpatov, and will be sent to the *Zoological Record*. The 1936 references appeared in full (in Russian) in the *Zool. Zh.* (1937), 16: 1022–77.

The Library of the Bureau of Animal Population, Oxford, has a growing collection of Russian reprints and some journals, and has had translations made of some papers. Copies of these translations can be purchased from the Bureau of Animal Population, University Museum, Oxford.

8. Transliteration of Russian names

The transliteration of names from the Slavonic (Cyrilic) into the Roman alphabet creates a certain amount of inevitable confusion, caused chiefly by the fact that English, French, and German authors each transliterate names into their own language on a phonetic basis. The generally accepted English criterion, that used by the British Museum, the *Review of Applied Entomology*, and in the transliteration of Slavonic names on to British maps, is given below. For reasons of bibliographical convenience I differ from this system in not printing the *ĭ* with its accent. The greatest confusion arises with the labial and sibilant consonants, and this reaches a climax when these elements occur at the beginning of a name, since it causes a change in the alphabetical arrangement of the bibliography. Included in parentheses after the approved equivalent are substitutions frequently found in the French and German literature. The use of these foreign equivalents is not "wrong", but the adherence to one standard in English publications seems desirable and convenient.

Russian	English	(Other)	Russian	English	(Other)
А, а	*a*		П, п	*p*	
Б, б	*b*		Р, р	*r*	
Ч, ч	*ch*	(*tsch, tsh, č, tch*)	С, с	*s*	
Д, д	*d*		Ш, ш	*sh*	(*sch, š*)
Е, е	*e*		Щ, щ	*shch*	(*šč, ch*)
Э, э	*é*	(*ê**)	Т, т	*t*	
Ф, ф	*f*		Ц, ц	*tz*	(*ts*)
Г, г	*g*		У, у	*u*	(*ou*)
І, і	*i*		ы	*ui*	(*y*)
И, и	*i*		В, в	*v*	(*-ff, -w*)
й	*i* (*ĭ*)		Я, я	*ya*	(*ja, ia, îa**)
К, к	*k*		Ѣ	*ye*	(*je, e, îe**)
Х, х	*kh*	(*ch*)	Ю, ю	*yu*	(*ju, u, îu**)
Л, л	*l*		З, з	*z*	
М, м	*m*		Ж, ж	*zh*	(*j, sh*)
Н, н	*n*		ь	'	(frequently omitted)
О, о	*o*		ъ	‘	(frequently omitted)

* These forms frequently found in American literature.

Frequently names ending in *-iĭ* are spelled *-y* (e.g. Brodskiĭ, Brodsky); with but very few exceptions, names ending in *-ow* and *-off* should be *-ov* in English (e.g. Formozov, Kashkarov, etc.).

9. References

The following list of 517 references is not intended to be a complete bibliography of Russian ecological work, or even of work dealing with community ecology in the sense used in this review. It is meant to give a guide to some of the main trends of this research, with emphasis rather on papers that contribute to ecological theory and method, rather than to purely economic or *ad hoc* research. It should be stated, however, that Soviet theory identifies general ecology with its application to the uses of mankind, and that there is a very large literature on special economic biological and epidemiological problems of which it has been impossible to give more than an indication here. A great deal of this literature contains valuable contributions to community ecology.

The omission of particular papers is explained partly by the accidents of library organization (Russian literature is not yet completely available in this country), and partly by reasons of space. On the whole it was thought to be preferable to give only those references which could be actually verified. In the case of certain papers of obvious importance this rule has been relaxed. The large number of reviews of Russian research published on the occasion of the recent twentieth anniversary of the Revolution provides good bibliographies in Russian to many of the subjects.

The titles given within square brackets are usually those of the summaries in non-Russian, modified sometimes to give a better sense of the original title. The titles of papers without non-Russian summaries are taken (or modified) in the same way from the table of contents in non-Russian, or else translated from the original. Authors' names are transliterated directly from the Russian; when this transliteration deviates from the version usually found so much as to cause confusion, the commonly found form is added in square brackets. Work bearing on Russian ecology not done by Russian workers, but of interest here, is indicated by the symbol §.

Certain publications have not been seen by me, and it is possible that they have translated summaries in non-Russian; these are indicated by the symbol ♯ after the abbreviation which shows the language the paper is written in. For this purpose the following abbreviations are used, a capital letter indicating the text of the paper, a small letter the summary in another language: *R*, *r*, Russian; *E*, *e*, English; *F*, *f*, French; *G*, *g*, German; *U*, *u*, Ukrainian.

The abbreviations for the periodicals mainly follow the system of *World List of Scientific Periodicals* (1934), but many journals are not in this *List*, while in the case of others it has been found desirable to use a different

abbreviation. The figure before the colon indicates volume (or number, where this is used, as frequently in U.S.S.R., in the sense of volume); the figures after the colon indicate pages. The number (in the ordinary meaning of subdivisions of a volume) is usually omitted from these references. But where, as is not uncommon, the paging starts afresh with each number, the number is included in round brackets before the colon. This practice of paging numbers separately appears to be dying out, but it adds to bibliography a complication of which the reader should take note.

[*Editor's Note.* As mentioned in the footnote on p. 354, the majority of the references have been checked from the original sources by Mr Charles Elton and Miss N. Waloff. Those which could not be checked, and for which the author is therefore responsible, are marked with an asterisk. The symbol † indicates that a translation is available in the Bureau of Animal Population.]

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REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 27, No. 2, August 1939)

THIS number contains eleven papers, an appreciation of the late Prof. Carl Schröter and the individual contributions to a symposium. With eight reviews, eight notices of vegetation and an account of the Easter meeting of the British Ecological Society, the number includes 287 pages altogether.

There are two contributions of special general interest: first, the Presidential Address to the Ecological Society by Prof. A. G. Tansley on British Ecology during the last Quarter Century: the Plant Community and the Eco-system; and secondly, seven contributions to a symposium on the Reciprocal Relationship of Ecology and Taxonomy. The various contributions to this symposium, following an introduction by A. G. Tansley, are: An ecologist appreciates and criticizes the taxonomist, by E. J. Salisbury; The use of ecological data in taxonomy, by O. W. Richards; Ecology and taxonomic differentiation, by J. S. Huxley; Detailed taxonomy and autecology, by D. H. Valentine; The measurement of ecological factors of use in taxonomy, by C. Diver; Ecology and taxonomy: the taxonomist's viewpoint, by V. S. Summerhayes and W. B. Turrill. A summary of a discussion which followed is also given.

Three papers deal with vegetation overseas. R. E. Vaughan and P. O. Wiehe continue their work on the vegetation of Mauritius with a description of the effect of environment on certain features of leaf structure, while A. P. G. Michelmore contributes a very extensive series of observations on tropical African grasslands. Also dealing with African vegetation but with that of Southern Nigeria alone, is the study by G. C. Evans on the atmospheric environmental conditions in the rain forest of that area. Another study of environmental factors is given in a paper by W. H. Pearsall and C. H. Mortimer on oxidation-reduction potentials in waterlogged soils, natural waters and muds.

Papers dealing with British vegetation include one on the ecology of a raised bog near Tregaron, Cardiganshire, by H. Godwin and V. M. Conway; another on the early growth of beech seedlings under natural and experimental conditions, by J. L. Harley; and a third, by E. Wyllie Fenton, on the vegetation of "screes" in certain hill grazing districts of Scotland. T. M. Harris briefly records changes in fenced grasslands in Wales and Dorothy C. Gibb describes the algal communities of Great Cumbrae in the Firth of Clyde.

In addition to the customary review of the *Journal of Animal Ecology*, reviews deal with British Empire vegetation, the record of the International Phytogeographical Excursion in Morocco and Western Algeria and the vegetation of Nigeria. There are also notices of recent papers on European, British and post-glacial vegetation. W. H. PEARSALL.

AN AMERICAN TEXT-BOOK

A. S. Pearse (1939). *Animal ecology.* 2nd edition, pp. xii + 642, 133 text-figures. McGraw-Hill Publishing Co. Ltd., Aldwych House, London, W.C. 2. Price £1. 10*s*.

The second edition of this well-known work is even longer than the first and there are few branches of zoology on which it does not have at least a word to say. One has the impression that the author finds it so difficult to define a science of ecology that everything is included in case the unknown key were accidentally omitted. As a result there is a certain lack of balance in the book; if some of the subjects dealt with briefly were omitted, the

others could be better treated. But it would be ungracious to complain of receiving too much if everything essential had been included and fully discussed.

The difficulty of writing a satisfactory book on ecology lies in the lack of any agreement as to what the subject is really concerned with. The definition (p. 1) "ecology is the branch of biological science that deals with relations of organisms and environments" would provide the title for an encyclopaedia but does not delimit a scientific discipline. There are three groups of biological facts which in various proportions find a place in most ecological studies. There is first what may be termed systematized natural history, which is very fully treated in the present work. Such subjects as adaptations of colour and behaviour, rhythms, reproductive activities, commensalism, etc., are all discussed with many interesting examples. The second group of facts, in this work mainly treated under the heading "ecological factors", concerns the effects of external stimuli, especially those like temperature, humidity, etc., on animal distribution and behaviour. The discussion of this might be improved. Too many facts belonging to the first group are interpolated and the examples of the quantitative effects of factors might be more numerous and arranged so that generalizations could more easily be made. Finally, there is a third aspect of the subject, the nature and composition of communities, and it is this side of all ecological works which is least satisfactory. This is mainly because far too little examination is made of "nature", while there is far too much description of "composition". Prof. Pearse devotes one page to discussing the "character of communities" whereas 212 pages are occupied by descriptions of "communities". He rightly criticizes those who describe animal communities in terms of dominants, influents, etc., defined only on superficial numerical data. There is usually no evidence at all that a so-called dominant animal has any influence on most of the other species living in the same habitat. On the other hand Prof. Pearse's classification in terms of *a priori* appraisal of physiographic features (e.g. B (*b*) Ponds, (1) Littoral, (*a*) Ponds with bare bottoms, (1) beach above water, (2) surface, (3) shore line, etc.) is open to at least equally strong criticism. It is clear that we do not know enough about the relations of animals to their environment to draw up a logical classification of this sort, and, even if we did, most of these so-called communities would be mere collections of animals which happened to be living near one another.

The reason why the treatment of animal communities is so unsatisfactory is that zoologists have taken over almost unmodified the ideas which they found ready to hand in botany. Amongst plants the competition for growing space ensures that any set of individuals in a small area is necessarily more or less integrated into a real community (i.e. the density of any species effects the densities of the others). In animals where this sort of competition is very little developed quite different principles must be thought out—an exercise still in its very earliest stages. As a general result, botanical ecology is to a considerable extent a science of communities, since almost any spatially defined group of plants is in some sense a community (where, as in the Arctic, vegetation is not continuous, it is notorious that the community concept becomes difficult to apply); in animals, on the other hand, almost the only true communities which have been described are the groups of hosts and parasites or of prey and predators. Whether these relationships alone will prove sufficient to define animal communities is still uncertain.

The chief criticism of the present work therefore is that it is a storehouse rather than a synthesis of existing information. Even as the former it has some disadvantages. The index is very inadequate, the names of authors and animals in particular not being included. Considering that it is a second edition, there are too many misprints (twenty-one have been noticed). It is unfortunate that the author has not usually followed the ordinary convention of printing the Latin names of genera and species in italics, though he has in a few places. The 65 pages of references should prove a useful feature, though they contain an extraordinary number of misprints and mistakes in citation.

O. W. RICHARDS

BIRD BIOLOGY

James Fisher (1939). *Birds as animals.* 281 pp., 10 charts and photographs. William Heinemann Ltd., 99 Great Russell St., London, W.C. 1; and Toronto. Price 12*s.* 6*d.*

It is not usual to find a book, which covers so wide a field so successfully as this one. Every aspect of birds, regarded as objects of zoological research and of amateur bird-watching, is dealt with clearly and concisely in a freely running style which manages to make masses of facts palatable. The two most impressive things about it are the way in which all aspects of bird research are shown to integrate, and the prodigious energy that has gone into the bibliography. For all this the pages do not become unreadable through their burden of references and illustrative names, though some difficulty has been experienced in deciding when and when not to give scientific names.

The first chapter on "Bird historians" and the second on "Bird history" serve to give two introductions to the main part of the book and to emphasize the close relation between the student and the thing studied. "Bird adaptation" (chapter 3) deals quickly with the general systematic state of affairs as regards birds, and finishes with some pertinent remarks on systematic criteria other than morphological ones. In chapter 4 the author passes on to the facts of variation and distribution. Both polymorphism and multiple character clines are dealt with and a rough summary given of the zoogeography of the various groups.

Chapter 5 continues logically to discuss the general effect of the environment and how this may interact with genotypes to produce variation. Also recent work is cited illustrative of limiting factors, whether directly physiological or ecological. A rough classification of major habitats (chapter 6) indicates the vast adaptive radiation of birds and it is shown how communities are zoned, stratified and defined in accordance with each particular set of circumstances.

When we come to the section on bird numbers (chapter 7), one of the most interesting ones to ecologists, we find a little more emphasis placed on the "student", but not at the expense of the "thing studied". Practically all the recent work done on censuses is reviewed and discussed competently (though it is not true to say that "we have no counts of the whole of the breeding population of any British bird cliff", since this has been done for the Isle of May), and the general reader is introduced to recent mathematical work on population equilibria, which he would find difficult to track down in digestible form elsewhere. In chapter 8 migration is summarized most efficiently, though the physiological work is confined to references to Rowan and Bissonnette. Ringing schemes are dealt with shortly.

Perhaps most interesting to the general zoologist is the chapter on colours and display, and this leads on naturally to the two last main chapters on territory and reproduction. In the first the reader is made familiar with modern views on sexual selection and with the important work of Hingston and Huxley on the use and classification of colours. Territory is discussed briefly but accurately and the chapter on reproduction includes the important distinction between ultimate and proximate causes of breeding. A wealth of information also is given on breeding habits and the psychological characteristics of the breeding bird. Finally chapter 12 on "Birds and Man" gives an interesting summary of introductions that have been effected and the efforts that are being made to securing a reasoned attitude towards protection.

The bibliography deserves nothing but praise although a courageous attempt to quote the titles of Aristotle's works in the original Greek has led to a sad mix-up of accents. The illustrations are to the point and a photograph of the author's taken on the Farne Islands deserves special commendation. Even the dust-cover has meaning! H. N. SOUTHERN.

THE RELATION OF MAN TO ANIMALS

F. Fraser Darling (1939). *A naturalist on Rona: essays of a biologist in isolation.* 137 pages, 28 photographs, and folding map. Clarendon Press, Oxford. Price 7*s.* 6*d.*

The organization and following up and digestion of ecological research suck so many ecologists back into the laboratory, the office or the museum, that it is satisfactory to have the observations and thoughts of a man who is constantly engaged upon actual field work and yet does not fall out of touch with the trends of ecological thought. The author, with his wife and son, spent some months on the remote island of North Rona, overcoming with great skill and boldness the considerable difficulties of getting there and living under bad weather conditions. This expedition went chiefly to study the large grey seal herd during its breeding time ashore; but many other subjects were also studied or pondered over, and some of them are described in this book.

Chapters deal with the life of the shore, the display of birds, the island itself and its ancient buildings, the social life of animals, the grey seals, wild life sanctuaries, and deer antlers (from mainland work), and with the feelings evoked by life in wild surroundings. The photographs are of very great beauty, and many are the result of much painstaking work in the field. A solid case is built up for including the social relations in any population study, at any rate of birds and mammals. The connexion between the size of colonies of sea-birds and their reproductive efficiency has already been discussed by the author in another book, and is developed a little further here.

Perhaps the most interesting feature of the present book is the author's outlook upon animal life, acquired and thought out in the course of a great deal of time spent among wild animal populations, and among un-industrialized human ones. These views colour strongly his plans for wild life sanctuaries, and he speaks out boldly upon many issues. On two practical points it is clear that some action should be taken. The legal freedom of the seas enables trippers to shoot sea-birds when they are not actually on land; and the rating laws continue to mulct any landowner who converts his estate into a sanctuary for animal life. Most people would subscribe to the following statement: "Law-making in the interests of wild life should take cognizance of the growing body of ecological work, but the greatest step forward will be when the State establishes wild-life reserves in the more remote parts of the country. They would serve the following public ends immediately: the wild life therein would be given breathing space for a time; the reserve would be a place in which the public could take pride and have healthy enjoyment; research into problems of conservation could be conducted with a scope and continuity of policy impossible at present."

Dr Darling discusses the creation of a Highland sanctuary or National Park. It is greatly to be hoped that when a National Park Authority comes eventually into existence, it will include within its organization some form of Biological Survey, which could coordinate the work of other institutions and of individuals, for the benefit of wild life conservation. How long must the faunal history of this island, and indeed of the British Commonwealth at large, be determined by the casual prejudices of smoking-room discussions or the unavoided clash of material interests? Why not begin to use in an intelligent way the new yardsticks and population concepts of animal ecology?

Dr Darling's essays, written on one of the few almost undisturbed parts of Great Britain, brings up these questions into one's mind, and also, very vividly and sincerely, the "rightness for themselves" of the animals that he describes. The book is very pleasant to read. The writing is at its best when it follows a plain course, and the author need not fear that the reader will flag if he omits some of the icing from his cake. We do not need metaphors about "fairy spears" to visualize the flashing mackerel in its course. Will not the clear vigorous language of Gilbert White suffice to display the natural dignity and unsentiment of wild animals in their cosmos?

When Dr Darling writes that "the aim of science should certainly be to remove the

mystery from natural phenomena, but not to take away wonder or that quality of nature which allows for the development and play of aesthetic appreciation", he is stating a very valuable truth. One feels that most ecologists, and nearly all zoologists, have lost this power of wonder, in their effort to tear away the mystery. CHARLES ELTON.

SHORT REVIEWS

Forest Bibliography to 31st December, 1933. *Part I. A. General forestry (by countries). B. Silviculture.* (1936, pp. 1–78. Price 5*s*.) *Part II. Silviculture (continued).* (1937, pp. 79–199. Price 12*s*. 6*d*.) *Part III. Forest protection.* (1938, pp. 200–74. Price 12*s*. 6*d*.) Compiled and published by the Department of Forestry, Oxford University. Obtainable from the Librarian, Department of Forestry, Oxford.

This useful series of bibliographies contains titles of most of the relevant publications in the English language, and a large number in French and German. (It does not cover other languages except where such publications have summaries in English, French or German.) Animal ecologists will find their chief interest in Part III, which is classified under the following sub-headings: Man, Animals (including bird and game preservation), Atmospheric influences, Fire, Weeds, Other agencies (various catastrophes, reclamation, etc.) and Fencing (including hedges). The number of reports dealing with damage by deer is interesting. One disadvantage of the bibliography is that, although the full titles and the abbreviated references are given, the authors' names are given without initials. However, the list will be found very useful by animal ecologists.

Forestry Abstracts. Vol. 1, No. 1, pp. 1–59. Imperial Forestry Bureau, Oxford, 1939. To be issued in four quarterly numbers; subscription direct to the Bureau. from residents of the British Commonwealth and Anglo-Egyptian Sudan, £1 p.a.; from other subscribers £1. 5*s*. p.a.

This periodical is the natural outcome of earlier lists of literature issued by the Bureau, and animal ecologists will find several sections of interest to them, e.g. Forest zoology and Forest protection. Besides abstracts, which are up to the usual high standard of the Imperial Agricultural Bureaux, there are short articles summarizing certain subjects. The résumé's of annual reports issued by various organizations are valuable, since such reports are often hard to get hold of. The abstracts are pleasantly got up and printed by the Oxford University Press.

Edmund Sandars (1939). *A butterfly book for the pocket: including all species to be found in the British Isles, with life-sized coloured plates, and life histories.* 332 small pages, many coloured plates and text figures. Oxford University Press, Amen House, Warwick Square, London, E.C. 4. Price 7*s*. 6*d*.

Those who have already used *A bird book for the pocket* and *A beast book for the pocket* will welcome another of these highly intelligent compilations by Mr Sandars, who refuses to be taken in by the protective jargon of specialists, and yet at the same time keeps a careful standard of accuracy. The present volume on butterflies makes the subject attractive and should enable observers not only to identify the species he meets, but to acquire the wide range of knowledge of their habits and habitats and seasonal cycles which identification makes possible. The author says, in a characteristic introduction: "They neither sting, bite

nor stink. Their capture is difficult enough to amuse, provides exercise not too violent for young or old, and is restricted to hours suitable for the former." So, teachers should find this book a valuable guide in field observation. There are small maps showing general distribution of species, charts of the annual cycle through the months, and a number of delightful illustrations.

Iceland Papers. Volume 1. *Scientific Results of Cambridge Expeditions to Iceland*, 1932–38. (17 reprints bound under one cover.) Oxford University Press, 1939. Price £1. 1*s*.

The British ecologist, who has very few opportunities of working upon communities that are not more or less drastically interfered with by man or his domestic animals, turns naturally to the nearest accessible parts of the Arctic and Subarctic regions. That is partly why a great deal of ecological survey and analysis has been done by summer expeditions to Greenland, Spitsbergen, Iceland, the Faroes, Lapland, and even Arctic Canada. In recent years Cambridge undergraduate exploring parties have concentrated a great deal on Iceland. Thirty-four men went out between 1932 and 1938 (some of them more than once), and the present volume of 17 reprints represents about half the scientific results. Five other papers are mentioned that were not obtained for the volume, and a further fifteen are in preparation for a second volume. The papers include glaciology, geology, geography, ecology and some taxonomy (spiders, Collembola, Oligochaeta). The ecology mostly concerns vegetation (the central desert, the island of Grímsey) and bird populations (gannets, habitat selection, food, etc.). Further workers in Iceland will find this volume worth its high price. The editor has done well to get so many diverse expeditions to pool their results in one convenient volume.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (at least 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, M. Dunbar, C. Elton, F. C. Evans, B. M. Hobby, M. Mare, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern, H. G. Vevers and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine and brackish

See also **252, 338, 343**

189. Daniel, R. J. (1938). "Report for 1938, Marine Biological Station at Port Erin, Isle of Man." 51: 1–36. University Press of Liverpool. Price 1*s.* 6*d.*

Oyster breeding experiments show that pure cultures of some species of small flagellates form better larval food than others. A list of additions to H. B. Moore's *Marine Fauna of the Isle of Man* contains species new to the area and further distributional and breeding records. An unusual Bryozoan larva is described.

190. Howes, N. H. (1939). "The ecology of a saline lagoon in south-east Essex." J. Linn. Soc. (Zool.), 40: 383–445.

The lagoon was formed by damming a creek of the river Roach nine years before survey took place. Chemical data and extensive collections of fauna and flora were made each month, January 1934–April 1935. Salinity was considerably less than that of sea-water and ratios of ions present altered, iron, phosphates and silicates being abundant and nitrates and nitrites occurring in traces only, suggesting that the organic decomposition cycle must be of unusual type. The carbon dioxide content was so low as to form a limiting factor to the production of phytoplankton. The fauna is described with notes on seasonal abundance. Qualitative and quantitative comparison is made with the surrounding marine fauna and that of Widewater Lagoon near the Adur estuary.

191. Moore, H. B. (1939). "The colonization of a new rocky shore at Plymouth." J. Anim. Ecol. 8: 29–38.

A newly made beach of limestone rock was observed for two years, and compared with a nearby old rocky beach. Plants and animals of the old beach are listed, and the colonization of the new beach is described. The process is one of gradual occupation, and conditions appear unsuitable for most species even after two years.

192. Rees, T. K. (1939). "A *Rivularia bullata-Balanus* community." J. Ecol. 27: 62–5.

A remarkable and quite isolated patch of the alga, *Rivularia bullata*, was found growing on the barnacle, *Balanus balanoides*, on rocks at Kennack Sands near The Lizard, Cornwall. This alga, occurring only sporadically elsewhere, is here the dominant plant, and seems to be completely dependent on the barnacle, the shells of which it colonizes when they are 4–6 months old. This observation emphasizes the importance of treating the community as a biotic entity rather than as a plant or animal one.

193. Purchon, R. D. (1937). "Studies on the biology of the Bristol Channel. II. An ecological study of the beach and the dock at Portishead." Proc. Bristol Nat. Soc. 8: 311–29.

The fauna of the beach associations was quite different from that of the dock, the latter being characterized by a number of Lamellibranchs. Analysis of the oxygen tension, salinity, *p*H and temperature of the water showed no difference for the two regions. At the beach the water was considerably more turbid and the wave action stronger. Laboratory experiments on Lamellibranchs showed an unfavourable reaction to turbidity and water motion, and these two factors were considered responsible for the failure of such animals to colonize the beach. Full lists of species included. (Part I of these studies is a general account by **C. M. Yonge** which immediately precedes this paper, pp. 310–11.)

194. Lloyd, A. J. (1938). "Occurrence of burbot in the estuary of the River Severn." Nature, Lond. 142: 1118–9.

Three specimens of *Lota vulgaris* obtained in the spring of 1938 constitute the first modern records of this fish in the West of England.

195. Rees, C. B. (1938). "Distribution of the polychaete *Ophelia cluthensis* McGuire." Nature, Lond., 142: 576–7.

Records of its occurrence in South Wales and Ireland extend its known range.

(*b*) Freshwater

See also **231**, **250**, **251**, **287**, **336**, **338**, **340**, **341**

196. Pearce, E. J. (1939). "*Deronectes griseostriatus* De G. and *Hygrobia tarda* Herbst. (Col.) from the same Irish locality." Ent. Mon. Mag. 75: 126.

These two water beetles were found in pools with a stony-gravel bottom which in places is sandy—the nearest approach to the "silt-bottom" of the customary *Hygrobia*-habitat.

197. Pearce, E. J. (1939). "New and additional Haliplid records for Eire and some notes on variation in British specimens of *Haliplus fulvus* F. (Coleopt.)." Ent. Mon. Mag. 75: 32–6.

Useful Irish distribution records.

198. Peters, B. G. (1938). "Habitats of *Limnaea truncatula* in England and Wales during dry seasons." J. Helminth. 16: 213–60.

The incidence of liver fluke is closely correlated with the population fluctuations of *L. truncatula*. The typical habitats of this snail are described in detail and methods of control suggested. The snail is very much more common in wet seasons since suitable habitats are then extended. A provisional map is given of the present distribution of live fluke in England and Wales.

199. Wailes, G. H. (1939). "The plankton of lake Windermere, England." Ann. Mag. Nat. Hist. 3: 401–14.

Samples of plankton were obtained by vertical hauls from 30 m. with a fine-meshed net, taken every two weeks during fifteen months. A list is given of species obtained together with notes on seasonal abundance and points of structual interest.

200. Reid, D. M. (1939). "On the occurrence of *Gammarus duebeni* (Lillj.) (Crustacea, Amphipoda) in Ireland." Proc. R. Irish Acad. B, 45: 207–14.

The common fresh-water species, *Gammarus pulex*, is replaced in the fresh waters of Ireland by a form exactly similar to the brackish-water form, *Gammarus duebeni*. *G. duebeni* is found in waters which vary greatly in their *p*H value, although no constant structural difference could be associated with variation in *p*H. Brackish-water forms of *G. duebeni* appear to be unable to breed in fresh water; spermatozoa did not seem to be affected by the change in salinity, but ova failed to develop after formation. The two physiologically distinct types are referred to as *Gammarus duebeni* α (the fresh-water type) and *G. duebeni* β (the brackish-water type).

201. Gardner, D. M. (1939). "A new planarian record for Scotland." Scot. Nat. 37–8.

The freshwater Turbellarian, *Planaria lugubris*, was locally common during 1937 and 1938 in E. Lothian. The worm is described.

(*c*) Land

See also **272**, **287**, **289**, **291**, **306**, **336**, **338**

202. Lack, D. & Venables, L. S. V. (1939). "The habitat distribution of British woodland birds." J. Anim. Ecol. 8: 39–71.

Survey by the British Trust for Ornithology, and observers organized under the Trust, of all British woodland birds in the main types of wood and main geographical regions of Britain. The habitat factors considered are: open as opposed to closed woods, presence or absence of undergrowth (called secondary growth), holes for nesting, tall trees for nesting or for song posts, and water. A comparative index of frequency of birds in different wood types recognizes eleven types: oak and mixed broadleaf, beech, birch, pine, larch, pine with secondary, pine without secondary, oak and beech with secondary, and oak and beech without secondary, Highland pine, and pine plantations. Both mixed broadleaf woods and natural pine are rich in birds, but plantations of both are poor. Eleven species are confined to broad-leaved woods, and five to coniferous. The former are mainly southern species, and the latter northern.

203. Nicholson, E. M. (1938–9). "Report on the lapwing habitat enquiry, 1937." Brit. Birds, 32: 170–91, 207–29, 255–9.

The main aim of the enquiry was to estimate factors governing the distribution of the lapwing (*Vanellus vanellus*) in Great Britain. Results showed a low correlation with geological features. High ground over 1200 ft. is avoided. Forty-five habitats were distinguished of which the commonest were arable land and permanent pasture above alluvial level. The effect of disturbance of breeding sites is hard to estimate, but it is thought that the lapwing suffers little, because of its mobility and of its habit of feeding at any hour of the twenty-four. A certain amount of quantitative data accompanies this work.

204. Temperley, G. W. (1938). "Cliff nesting of the house martin." Vasculum, 24: 127–8.

For some years there has been a considerable colony of house martins nesting on the cliffs on the Northumberland coast.

205. Wilson, G. F. (1939). "Insect pests of rhododendrons: their distribution in Britain." Proc. R. Ent. Soc. Lond. A, 14: 1–5.

The main pests of rhododendrons in Britain are the Tingitid bug *Stephanitis rhododendri*, the Aleurodid *Dialeurodes chittendeni*, Tortricid moths and the weevils *Otiorrhynchus sulcatus* and *O. singularis*. Distribution maps of two species are given and an appeal is made for records of the occurrence of three of the pests.

206. McDonogh, R. S. (1939). "The habitat, distribution and dispersal of the Psychid moth, *Luffia ferchaultella*, in England and Wales." J. Anim. Ecol. 8: 10–28.

This moth is small, 3–4 mm. long, wingless, case-bearing as a larva, and parthenogenetic. It lives on tree trunks where not shaded, and occasionally on stones, and feeds on lichens, especially *Lecanora*. Its range in England is enclosed by the isotherm of 62° F. for July, except where this month has more than 210 hr. sunshine, and it lies below 400 ft. elevation. Dispersal appears to be by wind, possibly up to several miles. It is inactive below 40° F., and positively phototrophic.

207. Wakely, S. (1939). "Some interesting Microlepidoptera." Proc. S. Lond. Ent. Nat. Hist. Soc.: 106–9.

Useful collecting and breeding notes.

208. Fletcher, T. B. (1939). "Plume larvae in May–June." Ent. Rec. 51: 76–7.

Useful habitat notes.

209. Klimesch, J. (1939). "A contribution to our knowledge of the biology of the species of the genus *Bucculatrix*, Zeller (Micro-Lepidoptera)." Proc. S. Lond. Ent. Nat. Hist. Soc.: 101–5.

General life-history. Includes cross-sectional diagrams of larval mines.

210. Niblett, M. (1939). "Notes on food-plants of the larvae of British Trypetidae." Ent. Rec. 51: 69–73.

A long list compiled partly from personal observations, and partly from published records mostly of Continental origin.

211. Yarrow, I. H. H. (1939). "The Aculeate Hymenoptera of a small isolated sand patch in Dorset." Proc. R. Ent. Soc. Lond. A, 14: 15–16.

The total area of the patch was about 28 sq. ft., but the area of available sand was only about 20 sq. ft. A list of 39 species representing 7 families is given.

212. Barnes, H. F. (1939). "Some gall midge species and their host plant range." Ann. Appl. Biol. 26: 318–47.

Dasyneura alpestris attacks certain species of the subgenus *Euarabis* and one other species which may belong to the subgenus *Lomaspora*. Other subgenera are not attacked. The chrysanthemum midge breeds on autumn flowering chrysanthemums, *C. indicum*, *C. rubellum*, *C. indicum* var. *azaleoides* (*C. azaleanum*) and *C.* Korean Apollo. Eggs were laid but no galls were formed on certain other plants of the *Chrysanthemum* genus and other genera. *Dasyneura tetensi* breeds only on black currant, *D. ribicola* on gooseberry only and *D. plicatrix* on *Rubus* spp. *Thomasiniana oculiperda*, *T. theobaldi* and *T. crataegi* are distinct species having a limited host range.

213. Cohen, M. (1938). "The tomato leaf miner and its control." J. Minist. Agric. 45: 460–2.

Includes life history and alternate host plant notes.

214. Collin, J. E. (1939). "On various new or little known British Diptera, including several species bred from the nests of birds and mammals." Ent. Mon. Mag. 75: 134–54.

Records of Phoridae, Anthomyiidae, Helomyzidae, Chloropidae, Ephydridae, Carnidae and Drosophilidae from little studied habitats.

215. Coulson, F. J. (1938). "Remarks upon British Clavicornia." Proc. S. Lond. Ent. Nat. Hist. Soc.: 75–80.

Useful collecting and habitat notes.

216. Walker, J. J. (1939). "Coleoptera in a limited area at Oxford." Ent. Mon. Mag. 75: 9–11.

A selection of the more interesting beetles from fully 300 species observed in an area of 30 acres of meadow and cultivated land.

217. Goodliffe, F. D. (1939). "Acridiidae (Orth.) in Worcestershire, E. Herefordshire and Shropshire, with a note on their ecology in the Malvern Hills." J. Soc. Brit. Ent. 1: 259–60.

Brief notes on habitat.

218. Petherbridge, F. R., Staply, J. H. & Thomas, I. (1938). "The beet eelworm (*Heterodera schachtii*, Schmidt.)." J. Minist. Agric. 45: 226–36.

Includes life history, host plants and methods of how the eelworms are spread.

(*d*) Small islands

See also **243**, **260**, **327**, **329**

219. Lockley, R. M. (1938). "I know an island." 300 pp., 17 maps and diagrams, and 49 photos. George G. Harrap & Co., Ltd., London. Price 10*s.* 6*d.* (Reviewed in J. Anim. Ecol. (1939), 8: 178–9.

Includes notes on Skokholm, Grassholm, Ramsey, Bardsey (Wales); the Blaskets (Ireland); Fair Isle, N. Ronaldshay (Scotland); also Heligoland, the Faeroes and the Westmann Islands.

220. Darling, F. F. (1939). "North Rona: a North Atlantic island." Proc. Roy. Instn. 30: 519–40.

An account of the topography and natural history of North Rona, dealing more especially with the author's research on the biology of the grey seal.

221. Bertram, D. S. (Editor) (1938). "The natural history of Canna and Sanday, Inner Hebrides: a report upon the Glasgow University Canna Expeditions, 1936 and 1937." Proc. R. Phys. Soc. Edinb. 23: 1–71.

Records by various workers upon different groups, prefaced by general descriptions of the topography and vegetation. The sections follow the conventional system of species lists with

habitat notes, etc. on most of them. Some attempt is made to refer these notes to the standard survey of vegetation: this is done especially for Hemiptera (W. H. R. Lumsden). There is a study (by A. J. Haddow) of the settledness of beetles under stones, done by counting and marking individually with paint the larger Carabids. The survey represents a considerable advance, both in completeness and the attention given to ecological data during collecting; but the results are not grouped ecologically so as to give a coordinated picture of the distribution of animal associations, or of their relation to plant associations. There is a good deal of data also for Sanday, Rhum and Òigh-sgeir.

222. Carrick, R. & Waterston, C. (1939). "The birds of Canna." Scot. Nat. 5–22.

Includes a list with distribution and habitat notes of 128 species definitely recorded from Canna since 1881, 47 of which breed there regularly. Since 1890 six species have decreased in number and a few have increased; introduced game birds have not become established. The vegetation has undergone little change which would influence the bird population.

223. Harrison, J. W. Heslop (1939). "Further contributions to our knowledge of the Lepidoptera of the Western Isles of Scotland. I. The Outer Hebrides." Entomologist, 72: 105–9.

A list of 83 species of moths.

224. Harrison, J. W. Heslop (1939). "The gall-making Hymenoptera of some of the Western Islands of Scotland." Ent. Mon. Mag. 75: 60–3.

Part of the survey of the Inner and Outer Hebrides organized by the Department of Botany, King's College, University of Durham.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

225. Scott, T. C. S. Morrison- (1939). "A key to the British bats." Naturalist, 33–6.

A valuable key and summary of distribution and field characters.

226. Scott, T. C. S. Morrison (1934). "Measuring mammals' tails." Ann. Mag. Nat. Hist. 3: 216–19.

Suggests that tail length be measured from the anus rather than from the angle obtained when the tail is bent up at right angles to the body as previously advocated. The exact method of laying out the animal for the new type of measurement is described and such anus measurements are found to be more constant than, and to fall within the extremities of, the old measurements.

227. Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1938). "The handbook of British birds. Vol. 2 (Warblers to owls). Pp. 1–352. (1939.) Ibid. "Vol. 3 (Hawks to ducks)." Pp. 1–387. Both volumes fully illustrated in colour and with text-figures. H. F. & G. Witherby, Ltd., 326 High Holborn, London, W.C. 1. Price £1. 1*s*. per vol. for subscribers to all five volumes; £1. 5*s*. for single volumes.

228. Parker, E. (1939). "Predatory birds of Great Britain." Brit. Field Sports Soc. Publication No. 37. 84 small pp., black and white illustrations. (London, British Field Sports Society, 3 St James's Square, S.W. 1. Price 2*s*.)

A handy book of small size devoting about a page to each species. Local names are given, followed by measurements and brief description, chiefly applicable if the bird is at close quarters, very short notes on the range (sometimes inaccurate, e.g. peregrine) and generalized remarks on food. There is a section giving general conclusions about gulls partly by "a well-known naturalist, whose word carries authority". The conclusion is that "all our gulls with the exception of the kittiwake are harmful in a greater or less degree", a statement which is general enough to be difficult to disagree with. The last 30 pages give the legal periods of protection for each species in each county.

229. Mellanby, H. (1938). "Animal life in fresh water: a guide to British freshwater invertebrates." 296 pp., 211 text-figs. London: Methuen & Co., Ltd. Price 8*s.* 6*d.* (Reviewed in J. Anim. Ecol. (1939), 8: 179.)

230. Browne, F. Balfour- (1938). "Systematic notes upon British aquatic Coleoptera. Being a corrected and revised edition of a series of papers which appeared in the 'Entomologists' Monthly Magazine' from 1934 to 1936. Vol. 1. Hydradephaga." London: Nathaniel Lloyd & Co., Ltd. Price 3*s.* 6*d.*

A systematic work containing many advances upon the standard text-books.

231. Marshall, J. F. (1938). "The British mosquitoes." London: British Museum (Natural History). Price £1.

An exhaustive and well-illustrated monograph with descriptions and keys to adults, larvae and pupae and notes on life-history, ecology, etc. Includes sections on feeding, oviposition, mosquito "control", flight range, rarity, parasitism and malaria in Britain.

232. Mosely, M. E. (1939). "The British caddis flies (Trichoptera). A collectors' handbook." London: George Routledge & Sons, Ltd. Price 21*s.*

The first complete work on the group in English since McLachlan's revision of the European Fauna (1874–84). Contains concise descriptions, keys, figures of wings and genitalia, but few distributional records.

233. Harrison, J. W. Heslop (1939). "The dragonflies of Northumberland and Durham." Vasculum, 25: 40–1.

Includes many distributional records omitted from the standard text-books.

234. Macan, T. T. (1939). "A key to the British species of Corixidae (Hemiptera Heteroptera) with notes on their ecology." Sci. Publ. Freshw. Biol. Ass. Brit. Emp. 1: 1–27. Price (to non-members) 1*s.* 6*d.* (Address: Wray Castle, Ambleside, Westmorland.)

The first of a series of illustrated pamphlets containing keys and references for identifying the lesser-known groups of British freshwater animals.

235. Bagnall, R. S. (1939). "Notes on British Collembola." Ent. Mon. Mag. 75: 21–8, 56–9, 91–102.

The third and fourth contributions of the series, introduces numerous species new to Britain and describes several new to science.

236. China, W. E. (1939). "Additions to the British Homoptera." Ent. Mon. Mag. 75: 41–56.

Important additions to the British list, with descriptions, figures and keys.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **190, 193, 200, 203, 241, 281, 290, 292, 293, 309, 311, 316–17, 320, 338, 340.**

237. Baker, J. R. (1938). "The relation between latitude and breeding seasons in birds." Proc. Zool. Soc. Lond. A, 108: 557–82. (Reviewed in J. Anim. Ecol. (1939), 8: 173–5.)

A generalized study of the breeding seasons of 254 species of birds shows the following scheme; in the tropics the height of the egg season follows roughly the path of the overhead sun, or is slightly before it. This means that to nearly 40° north and south of the equator there are two main peaks in the breeding season, occurring about February and August. Northwards the first of these is accentuated, southwards the second one. Many birds in the equatorial regions do actually breed twice a year, but the majority follow either one or the other of the seasons. There are other compli-

cations: in some orders of birds, e.g. Charadriiformes, Grallae, Herodiones, the breeding season gets earlier, from the boreal region southwards, but from the temperate region southwards it gets earlier again, so that its incidence in the tropics is just in front of the southward sweep of the sun. In the Accipitres, Coraciiformes and Passeres from the temperate zone southwards the breeding season continues to become earlier so that in the tropics it is just in front of the northward sweep of the sun. Generally speaking, little breeding takes place when days are less than 12 hr. in length, and almost none when they are less than 11 hr. However, there is no positive correlation with increasing day length, nor with particularly fast increase of day length. The significant coincidence of tropical breeding with the path of the overhead sun may indicate that light is a proximate cause of breeding, though the incidence of rainy seasons must also have an effect. In the temperate regions temperature and day length may be more important.

238. Smith, C. Horton- (1938). "The flight of birds." 182 pp., 17 plates and 30 text-figs. H. F. & G. Witherby, Ltd., London. Price 7*s.* 6*d.* (Reviewed in J. Anim. Ecol. (1939), 8: 178.)

239. Temperley, G. W. (1939). "Ornithological report for Northumberland and Durham for the year 1938." Vasculum, 25: 42–51.

Classified notes and discussion of weather and its effect on bird movements.

240. Lovern, J. A. (1939). "Captive eels: some observations on their behaviour." Salm. Trout Mag. No. 94: 56–7.

Notes on feeding and behaviour of eels in fresh and salt water.

241. Petherbridge, F. R. & Wright, D. W. (1938). "The cabbage aphis (*Brevicoryne brassicae* L.)." J. Minist. Agric. 45: 140–8.

Life history. The distance travelled by the winged forms appears to be considerable, several miles. Natural rate of increase is chiefly governed by climatic factors. Dry, warm conditions are very favourable for increase and the production and migration of winged forms. Cool, wet weather and especially heavy rainstorms reduce the numbers. Among the biological agencies are chiefly insect predators and secondarily insect parasites. Hover flies and gall midge larvae are among the more important predators.

242. Worms, C. G. M. de (1939). "Insects at light." Proc. S. Lond. Ent. Nat. Hist. Soc.: 80–4.

Includes brief descriptions of traps and discussion of main problems involved. See also **L. H. Ennis**, Proc. S. Lond. Ent. Nat. Hist. Soc.: 85–8.

243. Harrison, J. W. Heslop (1939). "The fate of pupae resulting from the Outer Hebridean *Pieris brassicae* immigrants of 1937." Entomologist, 72: 93.

Suggests that delayed emergence may account for erratic appearances of this butterfly in the Hebrides.

244. Edelsten, H. M. (1939). "*Lycaena dispar batavus* Obr. at Wood Walton Fen. 1938 (Lepid.)." Proc. R. Soc. Lond. A, 14: 6.

The colonies of the Dutch race of this butterfly, recently introduced into Wood Walton and Wicken Fens to replace the extinct British race, suffered rather heavily this spring owing to the inclement weather. The late frosts cut down the young dock leaves just as the larvae had emerged from hibernation, and ensuing drought delayed the growth of fresh leaves. The larvae consequently were short of food and it is believed some died of starvation. The insect appears to have remarkable powers of resistance and in spite of the adverse conditions sufficient butterflies emerged to produce a good stock of larvae.

245. Whitney, R. J. (1939). "The thermal resistance of mayfly nymphs from ponds and streams." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 44–8.

The thermal resistance of six species of Ephemerid larvae (*Baëtis rhodani, B. tenax, Rhithrogena semicolorata, Ecdyonurus venosus, Caenis* sp. and *Cloeon dipterum*) was measured by finding the temperature at which 50% were killed in 24 hr. Species exposed in nature to higher or more variable temperatures were more resistant than others.

246. Callan, E. McC. (1939). "Notes on the woodwasp, *Xiphydria dromedarius* F., on the cricket-bat willow." J. Soc. Brit. Ent. 1: 242–4.

The woodwasp, *Xiphydria dromedarius*, which appears to be more common than is generally supposed, was found on a number of occasions on or near the cricket-bat willow, *Salix alba* var. *caerulea*. Woodwasps were observed ovipositing in the trunk of a young bat willow recently killed by the honey fungus, *Armillaria mellea*, under circumstances such as to suggest that trees which are still green, but in which the wood is drying, are attractive for oviposition, while living trees are unsuitable.

247. Thorpe, W. H. & Caudle, H. B. (1938). "A study of the olfactory responses of insect parasites to the food plant of their host." Parasitology, 30: 523–8.

In the case of *Pimpla ruficollis*, a parasite of the pine shoot moth *Rhyacionia buoliana*, it has been shown that the parasites are only attracted by the oil of *Pinus sylvestris* when they are 3 or 4 weeks old, at which time the gonads become mature. Apparently the parasite finds the food plant of its host by a positive olfactory response which only develops when the eggs are ready for laying.

248. Callan, E. McC. (1939). "Assembling of *Thersilochus rufiventris* Brisch. (Hym., Ichneumonidae)." J. Soc. Brit. Ent. 1: 244–5.

Some hundreds of assembling males in a peculiar dancing flight around females ovipositing in the galls of the willow saw-fly.

249. MacLeod, J. (1939). "The seasonal and annual incidence of the sheep tick, *Ixodes ricinus*, in Britain." Bull. Ent. Res. 30: 103–18.

Tick incidence is greatest in spring and decreases markedly in early summer. Seasonal activity was found to be related to the air temperature, expressed as the weekly average of maximum temperatures. The limits of the air-temperature range corresponding to active tick infestation are 45 and 60° F.

250. Moon, H. P. (1939). "Aspects of the ecology of aquatic insects." Trans. Soc. Brit. Ent. 6: 39–49.

Stresses difficulty in correlating collecting results with physico-chemical factors. Shows how *p*H controls the arrangement of the fauna over a very large area, but is inadequate to explain details. Brings forward evidence that the substratum is the important factor in distribution. In lakes and streams, as the habitat evolves, there is gradual replacement of the food chains dependent on algae by those dependent on silt and detritus. The fauna is to a very large extent controlled by amount of erosion or deposition taking place. Silt may be used as an indicator of the intensity at which these processes are taking place and as a standard of comparison of diverse habitats.

251. Moon, H. P. (1939). "Importance of the substratum to the invertebrate animals on which fish feed." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 36–40.

A general discussion, with examples from the Avon and its tributaries, of the influence of the nature of the river bed on the distribution of the fauna.

252. Gillam, A. E., El Ridi, M. S. & Wimpenny, R. S. (1939). "The seasonal variation in biological composition of certain plankton samples from the North Sea in relation to their content of Vitamin A, carotenoids, chlorophyll, and total fatty matter." J. Exp. Biol. 16: 71–88.

Parallel chemical and biological studies of the plankton of the southern North Sea. The total plankton depends on three diatom outbursts, in May, August and October. Carotene, chlorophyll and vitamin A were detected in the gross plankton extracts, fucoxanthin only in few cases. The seasonal variation of chlorophyll most nearly coincided with the total mass of the plankton; carotenoids reached their peak slightly before the maximum biological development, while vitamin A content reached its maximum in the month after the spring diatom outburst.

253. Hawes, R. S. (1939). "The flood factor in the ecology of caves." J. Anim. Ecol. 8: 1–5.

Floods introduce a variable into the otherwise constant environment of caves. They bring about an annual rhythm in the life cycle of certain cave-dwelling animals. They introduce food into caves and they may cause the initial colonization of caves by fish originally living in above-ground waters. The discussion is based on observations in Jugo-Slavia.

254. Callendar, G. S. (1939). "Some interesting temperature anomalies for 1938." Quart. J. R. Met. Soc. 65: 137.

In most North Atlantic countries the mean temperature of last year was remarkably high and at several stations in North America, Scotland, and the Baltic countries it equalled or exceeded previous record values.

255. Keen, B. A. (1939). "What happens to the rain?" Quart. J. R. Met. Soc. 65: 123–37.

It is only in recent years that a true picture of the movement of water in the soil has been built up. In consequence, some of the traditional practices need revision, while others now have a different explanation. The new work has also clarified some of the concepts used in hydrology.

256. Manley G. (1939). "On the occurrence of snow-cover in Great Britain." Quart. J. R. Met. Soc. 65: 2–27.

Hitherto practically no information has been forthcoming with regard to the frequency with which a snow-cover may be expected on the uplands and mountains of Great Britain. Variations with altitude from year to year are very great. A relationship has now been derived between the mean temperature of the winter months and the average frequency of occurrence of snow-lying, which after test appears to be generally applicable to any given place over a period of years. It is necessary, however, to allow for several additional factors, notably quantity of snowfall, which influence the duration of snow-cover. It appears that, making these allowances, a reasonable estimate can be made of the frequency of snow-cover at the majority of places in Great Britain; also, of the extent to which the expectation of snow-cover varies with small fluctuations in mean winter temperature over a period.

257. Day, W. R. (1939). "Local climate and the growth of trees with special reference to frost." Quart. J. R. Met. Soc. 65: 195–209.

The type of forest is largely determined by the general climate, but local climatic conditions exercise considerable influence. The natural forest in this country is composed of species, some of which are relatively hardy to frost, whereas others are, in comparison, easily injured by it. The latter species usually form the final woodland, and their successful growth is made possible by the development of favourable conditions of climate and soil within woodland formed first of all by hardy species. Examples are given to illustrate the effect of overhead and side shelter on the temperature of the air over the ground. The influence of topography on frost is also illustrated and discussed. The effect of accessory factors, such as soil fertility, local warm or cold situations, and the general suitability of the exotic species to the climate to which they are introduced are also shortly discussed in relation to the occurrence of frost injury.

4. PARASITES

See also **198, 247, 248, 249, 309, 332**

258. Thompson, G. B. (1939). "A check-list and host-list of the ecto-parasites recorded from British birds and mammals. Part I. Mammals (excluding bats)." Trans. Soc. Brit. Ent. 6: 1–22.

Includes references and notes on comparative abundance. Gives special attention to parasites of the various island forms.

259. Thompson, G. B. (1939). "A list of the type-hosts of the Mallophaga and the lice described from them." Ann. Mag. Nat. Hist. 3: 241–52.

A further instalment of a list of bird hosts of lice and of the species which prey upon them.

260. Carrick, R. (1939). "Some parasites of birds and mammals from Canna." Scot. Nat.: 23–4.

Lists, with brief notes, of endoparasites (1 trematode, 1 cestode, 2 nematodes) taken from a sheep, and ectoparasites (4 Mallophaga, 4 Siphonaptera) taken from a rabbit, a dog, a pigmy shrew, pigs, starling, shag, nest of kittiwake and hen-houses on the Isle of Canna during July, 1936. One of the nematodes, *Bunostomum trigonocephalum*, was found also in a rabbit.

261. O'Mahony, E. (1939). "A preliminary list of Irish fleas." Ent. Mon. Mag. 75: 124–6.

List of 20 species with records of hosts.

262. Hopkins, G. H. E. (1939). "Straggling in the Mallophaga." Entomologist, 72: 75–7.

In most cases a given species of bird-louse has only one true host, though it may be found accidentally on unrelated hosts and more or less normally on closely-related species. As knowledge of systematics increases, the number of instances in which a given species is found to occur normally on more than one species of host is being reduced. When a species is found to be common to two hosts, a much closer relationship between them is required than was formerly thought to be the case. The dangers of accidental straggling due to imperfections in technique after the host has been shot, and casual straggling, e.g. in zoological gardens, are discussed; also normal straggling among sea-birds and water-fowl breeding or feeding in company, and true polyoecism.

263. Stunkard, H. W. (1938). "The development of *Moniezia expansa* in the intermediate host." Parasitology, 30: 491–501.

This Anocephaline Cestode, the adult of which infects rabbits, is found to develop to the cysticercoid phase when the eggs are fed to Galumnid mites. It is suggested that mites serve as intermediate hosts for *Moniezia* and probably for other Cestodes of this group.

264. McDonogh, R. S. (1939). "The parasites of *Luffia ferchaultella* (Stephens) (Lepidoptera, Psychidae)." Proc. R. Soc. Lond. A, 14: 41–6.

The larvae of this moth are not very highly parasitized, probably owing to the protection afforded by the larval case; but 13 species of 6 genera of Ichneumonidae, 6 species of 6 genera of Chalcididae, 2 genera of Braconidae, and 1 species of Proctotrupid were bred during the two summers of 1935 and 1936. A fairly large proportion of the species belonged to genera normally hyperparasitic, but it appears likely that they were not so in these cases.

265. Brindley, M. D. (1939). "Observations on the life-history of *Euphorus pallipes* (Curtis) (Hym.: Braconidae), a parasite of Hemiptera-Heteroptera." Proc. R. Ent. Soc. Lond. A, 14: 51–6.

It is well known that some Homoptera, notably the Aphididae, are extensively parasitized by Hymenoptera. The Heteroptera are apparently less subject to this kind of attack, but in recent years, in different parts of the world, certain Braconidae have been reared from Pentatomid or Capsid bugs. These parasites all belong to the subfamily Euphorinae which has a wide geographical distribution. It is still undetermined how far this group of Braconidae is specific for different bugs.

266. Andrews, H. W. (1939). "The family Cyrtidae (Diptera)." Proc. S. Lond. Ent. Nat. Hist. Soc.: 76–9.

A compilation not embodying original work, but bringing together a number of facts concerning their life-history etc. from scattered sources. The larvae are parasitic on spiders.

267. Goodliffe, F. D. (1939). "A joint infestation of Barley by *Lasiosina cinctipes* Mg., together with *Chlorops taeniopus* Mg. (Diptera, Chloropidae) and their Hymenopterous parasites." J. Soc. Brit. Ent. 1: 248–52.

25% of the shoots failed to produce normal ears, more than one-third of the Chloropid larvae were parasitized by a Chalcidid and 16% by a Braconid.

268. Hanson, H. S. (1939). "Ecological notes on the *Sirex* wood wasps and their parasites." Bull. Ent. Res. 30: 27–76.

A single generation of *Sirex* can support three generations of *Rhyssa* and one generation of *Ibalia*. Effects of parasitism by *Rhyssa* are cumulative. Superparasitism of *Ibalia* by *Rhyssa* is very frequent. Both parasites are efficient, but the combined effects of the two parasites result in a higher percentage of parasitism than when each is working alone. Parasitism by *Rhyssa* is highest when the *Sirex* is breeding in material under 3 in. in diameter, thus within reach of the *Rhyssa* ovipositor. The effective activity of *Ibalia* is limited to the egg and early larval stage of the host. Other factors in *Sirex* control are discussed, e.g. birds, fungi and climatic control.

269. Wilkinson, D. S. (1939). "On the identity of *Apanteles infimus* Haliday and of *Apanteles infimus* Haliday of Marshall (Hym. Bracon.)." Proc. R. Ent. Soc. Lond. B, 8: 53–60.

Includes distributional and host records.

270. Harrison, J. W. Heslop (1939). "A Dipterous parasite on the mollusc *Cochlicella barbara* on the Islands of Barra, South Uist and Canna." Entomologist, 72: 99.

A heavy percentage of the catch was parasitized by Dipterous larvae which emerged by boring a round hole in the shell and pupated in November and December. The adult has not been bred and the species is as yet undetermined.

271. Callan, E. McC. (1939). "*Cryptorrhynchus lapathi* L. in relation to the watermark disease of the cricket-bat willow." Ann. Appl. Biol. 26: 135–7.

Although this beetle has transmitted *Pseudomonas saliciperda*, the agent causing a watermark disease of willows in Holland, negative results were obtained in attempts to get this beetle to transmit *Bacterium salicis* the cause of watermark disease of cricket-bat willow in this country.

5. FOOD AND FOOD HABITS

See also **189, 241, 252, 253, 283, 305, 334**

272. Turner, J. S. & Watt, A. S. (1939). "The oakwoods (*Quercetum sessiliflorae*) of Killarney, Ireland." J. Ecol. 27: 202–33.

Deer, both the red (*Cervus elaphus*) and the Sika or Japanese (*Cervus nippon*) are very frequent around the lake. They remove the bark from the holly and graze the shoots. In winter they live mostly in the valley woods, where holly is often lopped to provide them with food. They are poached by burning *Molinia* pasture to attract them to the young grass where they are shot.

273. Thomas, J. F. (1938). "Food of nestling swallows." Brit. Birds, 32: 233–6.

Table of insects taken from adult swallows (*Hirundo rustica*) as they came to the nest to feed the young. The observations were conducted from mid-June to the end of August. Diptera were the commonest prey. It is recorded that one bird returned with 31 flies.

274. Thomas, J. F. (1939). "The food of the Little Owl. Derived from pellets, February 1936 to January 1937. Results of a year's observations of a single bird, its mate and family (South Downs, Seaford)." Discovery, 2: 94–9.

A detailed report on 368 pellets; among other prey includes records of 6 birds, 50 rodents, 1325 ground beetles, 1023 Staphylinid beetles and 5232 earwigs.

275. Eve, F. C. (1939). "Stomach pump for trout: a new substitute for autopsy." Salm. Trout Mag. No. 94: 33–7.

A useful method of obtaining stomach contents without killing the fish.

276. Soong, M. K. (1939). "Preliminary notes on the food of young trout and salmon parr." Avon Biol. Res. Ann. Rep. No. 6, 1937–8: 34–5.

137 trout and 17 salmon were examined, all from the same pool. Differences in the food of the two species were noted.

277. Carpenter, K. E. (1939). "Food of salmon parr." Nature, Lond., 143: 336.

Feeding is totally indiscriminate, but food organisms of sub-aerial origin are more numerous in the stomachs than aquatic types, and the number of Hemipteran plant pests suggests the desirability of encouraging the growth of trees and shrubs along the banks of streams.

278. Allen, K. R. (1939). "A note on the food of pike (*Esox lucius*) in Windermere." J. Anim. Ecol. 8: 72–5.

Pike over 30 cm. long fed almost entirely on other fish, principally perch (42% of those examined) and very little on trout (only 2%). A high percentage had empty stomachs.

279. Evans, A. C. (1938). "Physiological relationships between insects and their host plants. 1. The effect of the chemical composition of the plant on reproduction and production of winged forms in *Brevicoryne brassicae* L. (Aphididae)." Ann. Appl. Biol. 25: 558–71.

Under late summer conditions of light, the rate of reproduction is positively correlated with the nitrogen content of the host plant and, in particular, the protein content. The formation of winged forms is negatively correlated with the same factors. The chemical composition of the plant affects the amount of food eaten, the rate of growth, length of larval period and final pupal weight of *Pieris brassicae*.

280. Harrison, J. W. Heslop (1939). "The food-plants of *Pieris napi* in the Inner and Outer Hebrides." Entomologist, 72: 79–80.

Owing to the erratic distribution of possible food-plants, these differ from station to station, and even to some extent from isle to isle.

281. Evans, A. C. (1939). "The utilization of food by certain Lepidopterous larvae." Trans. R. Ent. Soc. Lond. 89: 13–22.

The food relationships of the larvae of *Phalera bucephala*, *Aglais urticae*, *Smerinthus populi*, *Malacosoma neustria* and *Pieris brassicae* have been studied. The coefficient of utilization of food falls steadily during the 1st and 2nd instar of *P. bucephala*; during the 3rd, 4th and 5th instars it fluctuates irregularly. The consumption, utilization and metabolism of food per gram of larva per day follow a similar course. The coefficient of growth increases until the middle of the 3rd instar and then fluctuates irregularly. About 90% of the water contained in the food is extracted during the first four days of larval life. The larvae of the species studied utilize and consume food at very different rates. The amounts of carbohydrate, fat and ash utilized per gram of larva per day differ very much in the four species. The nutritive ratio of the larvae is very much lower than that of certain growing mammals, i.e., cattle, sheep and pigs, and the difference seems to be correlated with the chemical composition of the tissues.

282. Blair, K. G. (1938). "Midges attacking other insects." Proc. S. Lond. Ent. Nat. Hist. Soc.: 84–5.

Includes survey of all known records. Though such records are as yet too few for certainty, they at least afford indications that each genus or species of midge that acquires this habit limits its victims to a particular order of insects.

283. Wilson, F. (1938). "Notes on the insect enemies of *Chermes* with particular reference to *Pineus pini*, Koch, and *P. strobi*, Hartig." Bull. Ent. Res. 29: 373–89.

No parasites of this scale-insect were found. The predators fall into three groups: (*a*) those which remove the wool from the *Chermes* before feeding, (*b*) those which enter the wool mass and attack the *Chermes* from within, and (*c*) those which do not enter the wool mass but attack the *Chermes* from outside. The major predators are *Leucopis obscura* (Ochthiphilidae), *Lestodiplosis pini* (Cecidomyidae), *Hemerobius stigma* (Hemerobiidae), *Wesmaelius concinnus* (Hemerobiidae) and *Exochomus quadripustulatus* (Coccinellidae).

284. Yarrow, I. H. H. (1939). "Observations on *Asilus crabroniformis* (L.) (Diptera)." Proc. R. Ent. Soc. Lond. A, 14: 17.

A female robber-fly was kept under observation for about an hour, during which time it made nineteen attempts upon passing insects, eventually securing the Staphylinid beetle *Philonthus aeneus*.

285. Hobson, R. P. (1938). "Sheep blow-fly investigations. VII. Observations on the development of eggs and oviposition in the sheep blow-fly, *Lucilia sericata* Mg." Ann. Appl. Biol. 25: 573–82.

Two meat meals are necessary for the development of mature eggs in the ovaries and neither plant materials nor animal excreta can replace the meat in the diet of the female.

286. Johnson, C. G. & Mellanby, K. (1939). "Bed-bugs and cockroaches." Proc. R. Ent. Soc. Lond. A, 14: 50.

It is widely believed that cockroaches eat bed-bugs and that some measure of control of *Cimex* may thus be affected, but experiments show that this is unlikely.

287. Reynoldson, T. B. (1939). "Enchytraeid worms and the bacterial bed method of sewage treatment." Ann. Appl. Biol. 26: 138–64.

The flora and fauna of a bacterial bed is discussed, a definite cycle of *Phormidium* being described. The worms feed primarily on *Phormidium* and are important agents in the spring off-loading of this alga. There is no summer off-loading owing to increased temperature and sunlight which lessens the effect of the worm depredations.

6. POPULATIONS

See also **2, 199, 203, 211, 220, 222, 244, 249, 252, 268, 318, 334, 337, 338, 339, 340, 341, 342**

288. Matheson, C. (1939). "A survey of the status of *Rattus rattus* and its subspecies in the seaports of Great Britain and Ireland." J. Anim. Ecol. 8: 76–93.

Intensification of efforts to eradicate rats (almost all black rats) on board ships has succeeded in reducing the number of ships requiring fumigation, and the number of rats per ship fumigated. Nevertheless, the undiminished black rat population on shore at several ports, and simultaneous decrease of brown and black rats at other ports, indicate that the black rat can maintain itself on shore without additions from the ships.

289. Taylor, W. L. (1939). "The distribution of wild deer in England and Wales." J. Anim. Ecol. 8: 6–9.

The population of wild deer is larger than generally recognized, and is increasing. Besides the two native species, the red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), of which the former is numerous in West Somerset and Devon, there is the fallow deer (*Dama dama*) of uncertain status, also three introduced species, the Japanese (*Sika nippon*), the Chinese muntjac or barking deer (*Muntiacus reevesi*), and the Siberian roe (*Capreolus pygargus*), which have escaped and are tending to increase their range and numbers. Where plentiful, deer cause losses to farms and woodlands. A list compiled from the notes of Forestry Commission officers gives the species and estimated relative local abundance in each county.

290. Warwick, T. (1939). "Some habits of pipistrelle colonies." Scot. Nat. 68–70.

Well established colonies of *Pipistrellus pipistrellus* in the rafters, etc., of cottages in the Tweed Valley, Selkirkshire, where they are very abundant, were under observation during July 1937, and May and June 1938. Large and small colonies may live under the same roof and still retain their individuality. Sounds of activity can be heard in the evening for about an hour before the bats emerge in a succession of small parties. In dull weather emergence is later, the parties are smaller and less time is spent on the wing. There is marked sexual segregation of adults during pregnancy and in May and June the main colonies of males were not located. Immature individuals of both sexes were sometimes found during those months with the females, but adult males did not join them till mid-July. A list of four other British species showing sexual segregation in summer is given.

291. Lister, M. D. (1939). "An account of the lapwing population of a Surrey farm." Brit. Birds, 32: 260–71.

Fluctuations in numbers of a particular area were studied over five years. Larger numbers were recorded during the last three years, which may be due to increase of grassland in the area. The first peak usually occurred in September and then fluctuations were erratic until January or February, when they declined to the normal breeding population. Flocks frequented grassland mostly, but would often move in numbers to arable land, especially when newly ploughed or after rain.

292. Southern, H. N. (1939). "The flocking of immature herons." Brit. Birds, 32: 346–9.

Flocking at a locality in Hertfordshire 8 miles from the nearest heronry occurred from spring to early winter, numbers rising to a peak from July to September. Practically all birds were immature.

293. Lack, D. (1939). "The display of the blackcock. I. Mid-April observations." Brit. Birds, 32: 290–303.

The "lekking" of the blackcock (*Lyrurus tetrix*) is described. Each male defends a special area of its own from which any other bird, however strong, will retreat, if attacked. This may reduce disturbance during copulation. An apparently pointless recrudescence of this display occurs in autumn.

294. Fisher, J. (1939). "The history of the Irish gannet colonies." Brit. Birds, 32: 314–19.

295. Marchant, S. (1939). "The Irish gannet colonies, 1938." Brit. Birds, 32: 320–5.

Census figures for Little Skellig and Bull Rock.

296. Southern, H. N. (1938). "Distribution of the bridled form of the common guillemot (*Uria aalge*)." Nature, Lond., 142: 951–2.

Field counts of the proportion of different varieties of the common guillemot in colonies of the British Isles indicate increasing percentages of the bridled form as one goes from south to north. English and Welsh colonies have less than 1%, 10–13% is characteristic of north Scotland, and 24% is recorded for Shetland. This cline is continued northward and southward of the British Isles. There appears to be another cline in *U. aalge* in the amount of melanin pigmentation on the back, northern birds being considerably darker than those in the southern part of the range.

297. Chislett, R. (1939). "The black-headed gull (*Larus ridibundus*) in Yorkshire." Naturalist: 125–30.

A detailed account of a survey of breeding colonies of the black-headed gull in Yorkshire, undertaken as part of the British Trust for Ornithology survey of this species.

298. Graham, M. (1938). "The trawl fisheries: a scientific and national problem." Nature, Lond. 142: 1143–6.

Trawl fisheries have been unprofitable for many years and the number of British fishermen has been considerably reduced since 1919. The relation of natural increases in stocks of fish to the original stocks may be compared to the relation of "principal" and "interest" in finance. Fishing often takes some of the principal as well as the interest, and stocks are then increasingly reduced. An analysis of general statistics of haddock and plaice catches shows that the increase of time and expense of fishing has greatly outweighed the increase in yield, so that much effort has been wasted, and the stock has been reduced to a low level. Estimates of increase of stock based on rates of reproduction, growth and mortality likewise indicate the desirability of a large cut in fishing expenses. The weight of a stock growing in an empty area follows the logistic S-shaped curve which is characteristic of the growth of many populations. As the fishery develops, the rate of fishing increases until the ratio of effort to yield becomes so great as to make further fishing unprofitable. A reduction in the rate of fishing, such as might be effected by limited quotas of each species for each area, is necessary for a satisfactory and economic solution of this problem.

299. Gerrish, C. S. (1939). "Scales of Avon trout and grayling." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 54–62.

Data on age and growth rates of 30 trout and 102 grayling, deduced from scale-readings.

300. Went, A. E. J. (1939). "Salmon in Éire: a study of the runs in 1937 and 1938." Salm. Trout Mag. No. 94: 44–55.

Discusses the salmon shortage in Eire in the last two years. Concludes that in 1937 three (grilse, small spring and summer fish) of the four most important age-groups were deficient and in 1938 all four (including also the large spring fish). In 1938 the fish were poorer in condition (weight/length ratio) than is normal. The only explanation appears to be unknown factors in the sea.

301. Hutton, J. A. (1939). "Wye salmon: results of scale-reading, 1938." Salm. Trout Mag., No. 94: 59–73.

Statistics of the catch, by rods and nets, of salmon in the river Wye. The total catch for the year was 2045 fish weighing 31,985 lb., the worst on record. 648 sets of scales were received for the determination of age. An abnormally high proportion (12·8%) were previously spawned fish. All classes, except the small summer fish, were below the average in condition (weight/length ratio). Hutton believes that the poor catch was due to depletion of the stock by unfavourable conditions of nature unknown in the sea.

302. Nall, G. H. (1939). "Notes on scales from Avon salmon smolts in 1938." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 16–26.

Age-determination from scales of 954 migrating salmon smolts trapped in the Avon in the spring of 1938. Approximately 90% were one year old, 9% two, and 1% three. Many had made rapid growth during the migration season.

303. Berry, J. (1939). "Account of hatching and stocking experiments." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 27–33.

A summary of experiments carried out for five consecutive years (1) to compare natural spawning with the sowing of artificially fertilized eggs of salmon and (2) to compare four methods of stocking with trout (with eyed ova, alevins, unfed fry and fed fry). He concludes that the experiments were on too small a scale to provide the required information, but the details are useful.

304. Lucas, C. E. (1938). "Some aspects of integration in plankton communities." J. Cons. Int. Explor. Mer. 13: 309–22.

A suggestive review of the numerous ways in which the zoo- and phytoplankton may interact. Stress is laid on non-predatory relationships.

305. Wimpenny, R. S. (1938). "Diurnal variation in the feeding and breeding of zooplankton related to the numerical balance of the zoo-phytoplankton community." J. Cons. Int. Explor. Mer. 13: 323–37.

There is a tendency for zooplankton to graze chiefly at night and shed ova by day, while diatoms show a reciprocal time relationship in their assimilation and reproduction.

306. Baweja, K. D. (1939). "Studies of the soil fauna, with special reference to the recolonization of sterilized soil." J. Anim. Ecol. 8: 120–61.

The work deals only with the soil macro-organisms belonging in the field of the entomologist, not with the micro-fauna or other micro-organisms dealt with by the micro-biologist. It was carried on at the Rothamstead Experimental Station from November 1935 to March 1937. Twelve plots of 9×9 in., of which four were controls, were arranged in four series to bring out the effect of inclosure with plates set 1 ft. in the ground, and of sterilization in February and in May. Sterilization was by removing the first foot of soil, baking it at 212° F. for 6 hr., and replacing it. The population in the sterilized soils equalled that in the controls in five months in the enclosed and in seven months in the unenclosed plots, and thereafter increased markedly above that of the controls. The insects, except for minor orders, increased beyond their normal numbers, while none of the other invertebrates except Araneida regained their normal density. Recolonization was neither from the sides nor from below, but from above. The possibility of damage to hothouse crops from large increases of injurious insects in sterilized soil is pointed out, and further investigation of soils sterilized by natural heat, as in the tropics, is suggested.

307. Davies, W. M. (1939). "Studies on aphides infesting the potato crop. VII. Report on a survey of the aphis population of potatoes in selected districts of Scotland (25 July–6 August 1936)." Ann. Appl. Biol. 26: 116–34.

Population figures from 43 centres analysed with a view to establishing any relation there might be with (*a*) proximity to winter host plants, and (*b*) meteorological conditions such as temperature, humidity and wind velocity. The results indicate special precautions necessary to ensure health in seed-potato stocks.

308. Harrison, J. W. Heslop (1939). "The recent scarcity of *Plusia iota*, *P. pulchrina* and *P. chrysitis* locally." Vasculum, 25: 31.

Although formerly abundant in Durham and Northumberland these three species of moths are now exceedingly rare.

309. Hardy, J. E. (1938). "*Plutella maculipennis* Curt., its natural and biological control in England." Bull. Ent. Res. 29: 343–72.

Life history, distribution and natural control of this moth, both physical and biotic. *Angita cerophaga* and *A. fenestralis* were the only parasites numerically important, but both apparently overwinter in other hosts. There is a key to the parasites and hyperparasites of *Plutella*. The upper limiting temperature of *Plutella* is approximately 40° C. and the lower for breeding purposes is about 10° C. Rain at certain critical times may be a controlling factor.

310. Blair, K. G. (1938). "Changes in the insect population of Britain during the last 100 years." Proc. S. Lond. Ent. Nat. Hist. Soc.: 61–7.

Deals with Lepidoptera and Coleoptera. The cases fall into two main groups: those species which are strictly local in their habits and which are readily exterminated in any particular locality by the disturbance of the ecological conditions pertaining to such locally, and those with a more general distribution throughout the country.

7. MIGRATION, DISPERSAL AND INTRODUCTIONS

See also **3, 6, 206, 218, 221, 238, 239, 241, 244, 253, 262, 289, 302, 306, 339, 342**

311. Southern, H. N. (1938). "The spring migration of the willow-warbler over Europe." Brit. Birds, 32: 202–6.

The rate of spread of the willow-warbler (*Phylloscopus trochilus*) is shown on a map by isochronal lines at fortnightly intervals. Isotherms of 48° F. are also shown and considerable conformity is noticed, though the birds tend to lag behind the spring at the start and to outstrip it towards the finish. The spread lasts from March 5th (Gibraltar) to June 1st (Inari), and covers 2500 miles in 88 days. It is suggested that the quicker start in this species than in the swallow may be due to the willow-warbler not taking prey on the wing.

312. Ticehurst, N. F. (1939). "The migratory status of the heron in Great Britain." Brit. Birds, 32: 242–6.

Most British herons (*Ardea cinerea*) are stationary, and winter immigrants from Europe are preponderantly immature birds.

313. Skovgaard, P. (1939). "Iceland birds visiting Scotland." Scot. Nat.: 61–7.

A list is given of birds ringed in Iceland during 1921 and recovered in Scotland, with ringing details and dates of recapture. Other countries in which recoveries of each species have been made during this investigation are noted for comparison. Of the 15,000 birds liberated, only a few (13 species) were recovered in Scotland. Migration maps are given for pintail, red-breasted merganser, and meadow pipit.

314. Thomson, A. L. (1939). "The migration of the gannet: results of marking in the British Isles." Brit. Birds, 32: 282–9.

First-year gannets (*Sula bassana*) migrate further south during their first winter than adults.

315. Lockley, R. M. (1939). "The sea-bird as an individual: results of ringing experiments." Nature, Lond., 143: 141–4.

Skokholm Island, on the coast of Pembrokeshire, has been used as a bird observatory station for a number of years. Study of individual birds by ringing has produced much valuable material for life histories. The Manx shearwater, storm petrel and puffin have been shown to have long incubation and fledging periods, followed by an abrupt desertion of the young, which then fast for some days before making their way to the water. Shearwaters winter as far south as the Bay of Biscay, but return in February to occupy their former nesting sites. Pairing appears to be for life, but young birds do not breed until nearly two years old. Birds taken to the Faeroe Islands and to Venice have returned within a very short time to their nests on Skokholm. At the present time, this station is being carried on entirely by voluntary support, but it managed to ring more than 6000 birds in 1938.

316. Parker, H. W. (1939). "Marine turtles as current indicators." Nature, Lond., 143: 121.

The occurrence of seven turtles, four of them identified as common loggerheads, on the British coasts during December 1938 suggests that there has been a strong drift of warm surface water into the English Channel from the south-west.

317. Russell, F. S. (1939). "Turtles in the English Channel." Nature, Lond., 143: 206–7.

The presence of marine turtles in British waters might be associated with an extension of the northern range of these animals and a consequent shifting of the centres of distribution.

318. Smith, E. P. (1939). "On the introduction and distribution of *Rana esculenta* in East Kent." J. Anim. Ecol. 8: 168–70.

Twelve specimens introduced in the winter of 1934–5 increased to large numbers, and, in $3\frac{1}{2}$ years spread over a square of about 28 miles, mostly connected by water. They migrate in June and October, occupying a small pond for a year, abandoning it one or two years, and returning in large numbers. In 1938 their very loud singing suddenly abated, and, though they are still numerous, it is suggested that they are on the way to the semi-extinction of earlier introductions elsewhere in the British Isles.

319. Dahl. K. (1939). "Homing instinct in salmon: the case for separate river races." Salm. Trout Mag. No. 94: 19–26.

A résumé of the evidence for the return of salmon to the rivers in which they were reared.

320. King, G. M., Jones, J. W. & Orton, J. H. (1939). "Behaviour of mature male salmon parr, *Salmo salar* juv. L." Nature, Lond., 143: 162–3.

Groups of mature males taken from the River Alwen in Wales had entered a swift stream-like overflow from a set of salmon-keeping tanks, in which large mature females were being stored. It is suggested that mature male parr are more active than other parr and show different migrational movements; they may also be attracted chemotactically to the mature females.

321. Hartley, G. W. (1939). "Salmon caught in the sea—the island of Soay and Ardnamurchan, 1938." Fisheries, Scotland, Salmon Fish., 1939, No. 1: 1–16. (Edinburgh: H.M. Stationery Office. Price 9*d*.)

Fish were weighed and measured by a new, quicker method, using a board and canvas pocket. Ardnamurchan smolts were the biggest yet found on the west coast. They differ from Soay smolts and have different migration routes.

322. Tulloch, J. B. G. (1938). "Insects and other things which arrive by steamer from overseas." Entomologist, 72: 114–16.

A list of Arthropoda found in banana crates from Brazil and brought to Stepney Borough Museum, 1937.

323. Dannreuther, T. (1939). "Migration records, 1938." Entomologist, 72: 119–22.

Includes table of estimates of district abundance during 1938, also additional records.

324. Dannreuther, T. (1939). "Migration records, 1938." Entomologist, 72: 9–15.

A summary of the movements of migratory Lepidoptera recorded in 1938 in the British Isles, followed by some Continental observations and a general summary of records of abundance with dates of first and last appearances.

325. Garrett, F. C. & Harrison, J. W. Heslop (1939). "Is the green-veined white ever an immigrant?" Vasculum, 25: 33–4.

Discusses evidence for and against migration of this butterfly.

326. Williams, C. B. (1939). "The migrations of the cabbage white butterfly (*Pieris brassicae*)." 7th Int. Kongr. Ent., Berlin, 1938, Verhandl., 1: 482–93.

The cabbage white butterfly is a regular migrant, the most conspicuous movement in Europe being in a southerly direction through central Europe. These flights must originate somewhere to the north of this, but so far there is no clue to the exact area, or areas, from which they come. Outbreaks of caterpillars have been recorded at times in Southern Scandinavia doing severe damage to Cruciferae, but no one has yet recorded any directional movement of adults.

327. Harrison, J. W. Heslop (1939). "*Argynnis aglaia* and *Pieris napi* flying out to sea." Entomologist, 72: 59.

Records observations on Rhum and Longay. Some of the fritillary butterflies soon returned to land, but a few sped far across the water and were lost to view. The green-veined white, however, invariably returned to the cove, or rockledge, supporting its food-plant. The possible bearing of these observations on statements concerning alleged immigrations of this butterfly is deliberately left for "consideration and appreciation of others".

328. Wakely, S. (1939). "Notes on *Pyrausta nubilalis*, Hubn." Ent. Rec. 51: 3–5.

This moth, known in America as the European corn borer, has always been considered to be a casual immigrant as far as Britain is concerned. A small colony appears to have established itself at Benfleet, Essex, on *Artemisia vulgaris*, its chief host-plant in Belgium and N. France.

329. Harrison, J. W. Heslop (1939). "The northward advance of *Plusia moneta* L." Vasculum, 25: 31.

This moth has now reached Rhum, but searches for it on the neighbouring islands of Eigg and Muck were profitless. See also **F. C. Garrett**, 1938, Vasculum, 24: 115; **J. W. Harrison**, 1938, Vasculum, 24: 101–2.

330. Daniels, E. T. (1939). "*Limnophilus affinis* Curt. (Trichoptera): an immigrant?" Entomologist, 72: 46–7.

Circumstantial evidence that an immigration of this caddis fly may have taken place at Great Yarmouth on 11 October 1937.

331. Waterston, A. R. (1939). "Migratory locust in Scotland." Scot. Nat.: 48.

An immigrant female *Locusta migratoria*, belonging to the solitary phase, was found on the island of Rousay, Orkney, in 1938. Locusts normally migrate during the social phase of their life-cycle.

332. Davies, W. M. & Whitehead, T. (1938). "Studies on aphides infesting the potato crop. VI. Aphis infestation of isolated plants." Ann. Appl. Biol. 25: 122–42.

Investigations to ascertain the extent of the migrations of winged aphides, their ability to detect individual plants, the development of aphis population following colonization, and the extent to which virus diseases may be transmitted to isolated plants by winged aphides.

333. Moon, H. P. (1939). "Movements of the invertebrate fauna over the substratum." Avon Biol. Res., Ann. Rep. No. 6, 1937–8: 41–3.

Data on the rate at which animals of the stream bed re-colonize bare stones.

334. Macleod, J. (1938). "The tick problem." Vet. Rec. 50: 1245–50.

In areas where the British sheep tick, *Ixodes ricinus*, has been long established, there is no consistent trend of increase or decrease, and the tick population level fluctuates about a constant value. The invasion of new territory often gives the impression of great increase, but on account of the relatively small areas invaded, this phase of the problem is of little importance. Spread is almost entirely effected by hosts, and the survival of ticks in new territories is largely controlled by microclimatic factors, of which humidity is the most important. Recent extension of tick territories is due to the development of favourable vegetational conditions away from cultivated types and towards a heath or moor type. Sheep dips, particularly those of vegetable origin, are useful means of prevention of tick invasion, but control will lie in the correct management of pastures marginal to tick territories. The recent movement to exterminate deer as tick carriers in certain areas is of negligible value as a control measure, since the density of deer is too low to be effective in tick spread, and the habits of deer are such that their ticks are not scattered widely, as is the case with sheep.

335. Small, T. (1939). "On the first outbreaks of potato eelworm (*Heterodera schachtii*, Schmidt) in Jersey." J. Helminth. 17: 39–40.

Tests indicated that Jersey was entirely free of this parasite in 1935 and all potatoes entering the Island since then have been certified free of the pest. In 1938 an outbreak was reported from four small potato areas and later among tomatoes. Infection is heavy and appears to be several years old. It may be necessary to use systematic crop rotation to eradicate the pest.

8. REPORTS OF ORGANIZATIONS

336. Lancashire and Cheshire Fauna Committee (1939). Twenty-fourth Annual Report and Report of the Recorders for 1937. 30 pp.

Notes on birds and Lepidoptera, some of which contain ecological information. There are special reports on the red-backed shrike (*Lanius colusio*), the magpie (*Pica pica*), the coot (*Fulica atra*), and the chiffchaff (*Phylloscopus collybita*).

337. Bureau of Animal Population, Oxford University (1938). Annual Report, 1937–8. 36 pp.

The introduction includes a classification of the factors of reproduction and mortality in relation to population dynamics, and a review of the general organization of research required for population investigations. Separate sections summarize work on vole populations, game-birds and rabbits, enquiries into North American wild life cycles, and the results of some other surveys in Great Britain. There is a list of periodicals added to the library, mostly dealing with wild life conservation and allied subjects. It is announced that the Bureau is making translations of some Russian ecological papers, copies of which can be obtained from the Bureau.

338. British Trust for Ornithology (1939). Fifth Report, Spring, 1939. 33 pp.

Reports are given in some detail of recent co-operative enquiries. The lapwing (*Vanellus vanellus*) habitat enquiry. Inquiry into the distribution of the corn-crake (*Crex crex*): 1200 returns and 1000 other communications show a general decrease, less marked in Scotland. A certain number of isolated increases are reported. The inquiry is being continued. Survey of breeding colonies of the black-headed gull (*Larus ridibundus*): the most striking fact is the colonization that has taken place inland during the last 25 years. Coastal colonization has also gone on in the west. Song period enquiry, which is being continued. Sample census of heronries. Bridled guillemot (*Uria aalge*) enquiry. Local distribution and habitat enquiries. Woodcock (*Scolopax rusticola*) enquiry. Woodland bird enquiry: it is noted that many of the special British forms of birds (21 out of 37) are woodland inhabitants. Lists are given illustrating this. Fulmar (*Fulmarus glacialis*) enquiry: figures are given showing details of the fulmar's spread since 1878, when the first colony apart from St Kilda was founded. New enquiries are being undertaken, one into the status of the redshank (*Tringa totanus*) and another into hatching and fledging periods. (For fuller notices on some published enquiries see **203**, **296**.)

339. Skokholm Bird Observatory (1938). Report for 1938. 22 pp. (Address: Skokholm Bird Observatory, Dale, Haverfordwest, Pembrokeshire, Wales.)

Some of the most interesting information concerns the attempts to exterminate the wild rabbit (*Oryctolagus cuniculus*). After a last attempt to infect them with myxomatosis, which again failed to spread, cyanogas was used from November to the end of February with promising results. The house mouse (*Mus musculus*) is approaching a peak in its numbers, to which it has gradually been rising since 1935. One further experiment in homing was undertaken, a manx shearwater (*Puffinus p. puffinus*) being released at Le Havre on 16 April, and recorded back in its burrow on 15 May. There is a brief summary of the course of bird migrations with notes on weather conditions, and a number of notes on particular species. 3685 shear-waters were ringed; three ringed as nestlings in 1937 were recovered in July and August, 1938, showing that first year birds visit the colony, but do not breed. One shearwater ring has been found in the stomach of an angler fish (*Lophius piscatorius*).

340. Freshwater Biological Association of the British Empire (1939). Seventh Annual Report for the year ending 31 March 1939. 97 pp. Price (to non-members), 1*s.* 6*d.* (Address: Wray Castle, Ambleside, Westmorland.)

The work of the Association, with its headquarters at Wray Castle on Lake Windermere, is described, with particular emphasis on the relation of pure research to problems of water supply and fisheries. A new departure is the study of the bacteriology of freshwaters. The report includes six semi-popular articles by various members of the staff on the work now in progress. The first two refer to the algal cycle and its controlling factors. M. Rosenberg: "Changes in the phytoplankton". C. H. Mortimer: "Changes in physical and chemical variables". C. B. Taylor: "Bacteria in freshwaters". C. H. Mortimer: "Lake deposits". T. T. Macan & H. B. N. Hynes: "Faunistic studies". E. B. Worthington & G. H. Swynnerton: "The growth of brown trout".

341. Avon Biological Research (1939). Annual Report No. 6, 1937–8. 67 pp. (University College, Southampton. Price 2*s.* 6*d.*)

Contains a general account of the activities of the freshwater station at Southampton during the year. They included trapping smolts, experimental rearing of smolts, hatching and stocking experiments and work on the general ecology of the Avon. There are nine more detailed reports on work in progress.

342. Yorkshire Fishery District, Board of Conservators (1939). Seventy-second Annual Report on the Salmon, Trout and Freshwater Fisheries in Yorkshire. (By **W. T. Clarke.**) 43 pp.

Gives figures for the annual catch in 1938 by nets and rods in sea, estuary and river of salmon (721 fish weighing 10,964 lb.) and migratory trout (1561 fish weighing 5529 lb.), a decrease of some 70% on the previous year. Notes on brown trout and other freshwater fishes, fish passes to enable migrating fish to surmount obstructions, the Keld Head hatchery and re-stocking operations, and pollution.

343. Scottish Marine Biological Association (1938). Annual Report, 1937–8. 23 pp.

Short accounts of the work on herring, plankton, lobsters, molluscan ecology and shell formation in the crab *Carcinus maenas* are given. A list of marine nematodes from the Clyde Sea Area includes habitat notes.

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